ENVIRONMENTAL STABILITY: ITS EFFECT ON STREAM BENTHIC COMMUNITIES

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Russell G. Death

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Dedicated to the 442, 848 invertebrates who gave their lives to make this study possible

ABSTRACT

The effects of environmental stability on benthic community structure were examined at eleven sites (ten streams and a wind-swept lake shore) in the Cass-Craigieburn region, New Zealand. Physicochemical conditions, apart from stability, were similar at all sites. Epilithic biomass was considerably higher at the more stable sites, but the composition of periphyton communities, and amounts of benthic organic matter present were more strongly influenced by the nature of the riparian vegetation than by stream stability.

Invertebrate species richness and density were markedly higher at the more stable sites, but species evenness peaked at sites of intermediate stability. Sites of high and low stability had species-abundance distributions that were modelled best by the log series distribution, whereas sites of intermediate stability were modelled best by the log normal distribution. Communities were dominated by a common core of taxa at all sites, although their relative abundances changed markedly between sites. Differences appeared to be related to a combination of environmental stability and site location (e.g., in forest or grassland). Persistence of the dominant taxa was high at all sites, but persistence of the entire fauna was higher at the stable sites.

Communities at the more unstable sites appeared to be less complex and were expected to have higher resilience (i.e., ability to recover from disturbances) than those at more stable sites. Analysis of the local stability of community matrices indicated that matrices were unstable at all sites, although those at the less stable sites had eigenvalues closer to the stability criterion. These sites also had higher theoretical resilience if eigenvalues beyond the criterion for stability were ignored. An experimental study of recovery rates in four streams of different stability did not provide any support for higher resilience at less stable sites, all communities recovered at a similar rate. The composition of invertebrate communities at several of the less stable sites could be attributed to simple random colonisation processes, but community structure at the stable sites could not, although the reason for this remains unclear.

Finally, food web structure was strongly influenced by environmental stability, with shorter food chains, higher connectance and an overall more variable structure in the less stable streams. This may be a direct response to stability *per se* or mediated by it indirectly through its effect on the food base of the communities.

CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

One of the central issues in community ecology throughout this century has been whether or not the collection of species populations in a particular habitat can be considered a structured entity (Roughgarden, 1989). Are they simply the species that happen to arrive at a site, or are they a special subset with properties that allow their coexistence? Answers to these questions were initially split between two schools of thought, one founded by Elton (1933), who believed a community was an organised entity with limited membership, and the alternative view initiated by Gleason (1926) that communities resulted from a combination of chance immigrations and the effects of fluctuating and variable environments.

During the 1960s and 70s advances in theoretical ecology, further developed the view that communities were entities of limited membership structured by competition and to a lesser extent predation (Cody & Diamond, 1975). Attempts during the 80s to find empirical support for the concepts and theories proposed in the 1960s and 70s met with limited success, however (Roughgarden, 1989). Because of this, there has been a swing away from the largely deterministic view of community structure to one placing more emphasis on non-equilibrial and stochastic processes (Strong *et al.*, 1984; Diamond & Case, 1986). This swing has not been complete however, and both the empirical (Schoener, 1986a) and theoretical (DeAngelis & Waterhouse, 1987) nature of communities are now seen to be more pluralistic with most lying somewhere on a continuum between the extremes where communities will be structured entirely by deterministic processes, or solely by stochastic processes (Giller & Gee, 1987; Cody, 1989).

Within the context of this debate over the relative importance of stochastic and deterministic forces, the question of what determines species diversity and how this affects community stability (i.e., the ability of the community to persist in the face of disturbances) has been one of the major topics of contention. The stability/complexity dilemma, i.e., whether more or less complex communities have greater stability has also evolved through the latter part of this century (May, 1981; McIntosh, 1987). During the 1950s and 60s it was generally held that more complex communities should be more stable (MacArthur, 1955; Elton, 1958), however, the mathematical modelling approaches of the 1970s (e.g., Gardner & Ashby, 1970; May, 1972) led to the converse view, and now less complex communities are generally considered to be more stable (May, 1981; Pimm, 1982) at least in theory. Debate centring on the stability/complexity relationship has however, also become pluralistic, and it is now acknowledged that both the scale of disturbances, and the specific nature of the communities will alter the effects of increased complexity on stability (e.g., DeAngelis, 1975; Pimm, 1982).

Although the concept of diversity has been useful for comparing ideas about

communities of different types, it incorporates very little information on the structural and functional nature of a community. To this end, the emergence of food web theory (Cohen, 1978) has been seen as a major advance (Roughgarden, 1989). Thus, while it is still possible to compare communities of very different types, much of their structural and functional nature is retained. Food web studies have uncovered a number of general patterns common to a broad spectrum of communities, although the underlying reasons for these patterns are not so clear (Lawton & Warren, 1988; Lawton, 1989).

Whereas the main stream of ecology has advanced through both the development of theory and the empirical testing of theories, lotic ecology has until very recently remained an essentially descriptive science, seemingly oblivious to the theoretical basis of ecology as a whole (Barnes & Minshall, 1983; Hildrew & Townsend, 1987). Nevertheless, although it was slow to develop, a dichotomy between the deterministic and stochastic views of community structure has also arisen in studies of stream invertebrate assemblages. The view that benthic communities are most strongly influenced by stochastic forces, such as disturbances has been propounded by some (e.g., Reice, 1985; Lake & Barmuta, 1986; Lake *et al.*, 1988), whereas others (e.g., Hart, 1983; McAuliffe, 1983; Minshall *et al.*, 1985) have considered that benthic communities lie on a stochastic - deterministic continuum, and that their position on this continuum is related to environmental stability. Proponents of this latter view, also emphasise temporal and spatial scale as important determinants of the relative position of communities along this continuum. Even some workers who consider that most stream communities are structured predominantly by stochastic events do admit that it is at least theoretically possible for deterministic communities to develop in more "benign" (*sensu* Peckarsky, 1983) environments (e.g., Lake & Barmuta, 1986). The principal bone of contention therefore seems to be whether or not, such benign conditions ever occur in stream environments.

Discussions about lotic community structure have to date been concerned mainly with the importance of competition (Hart, 1983; McAuliffe, 1983) and predation (Peckarsky, 1983, 1984) as structuring forces in benthic communities. Very little consideration has been given to other topics central to discussions in main-stream ecology, such as the stability/complexity dilemma, food web theory, community persistence and resource partitioning. Although some exceptions to this include Bruns & Minshall (1983) (stability/complexity dilemma), Hildrew *et al.* (1985) (food web theory), Meffe & Minckley (1986) and Townsend *et al.* (1987) (community persistence), and Hildrew *et al.* (1984), Tokeshi (1986), Tokeshi & Townsend (1987) and Rader & Ward (1989) (resource partitioning).

Furthermore, although both the stability/complexity dilemma and food web theory have received considerable theoretical investigation in main-stream ecology, there have been few empirical studies undertaken to test these theories. Food web investigations in particular appear to be based almost entirely on 113 food webs (of variable quality) collated from the literature (Briand & Cohen, 1987) (although several more recent studies have begun to redress this problem, for example, Pimm & Kitching (1987), Warren (1989) and Winemiller (1990)). One aim of my study was therefore to collect more empirical data relating to food web theory, in particular, what influence environmental stability has on food web structure.

The central objective of my study was therefore to investigate the effect of environmental stability on benthic community structure by comparing communities in streams of differing environmental stability, but similar physicochemical conditions. In particular, I set out to examine whether these communities could be considered unstructured assemblages of chance colonists, or whether differing levels of environmental stability placed or lifted constraints on community structure. That is, do the communities of more unstable streams have any particular characteristics that allow them to persist (if they do) in the face of continual disturbance.

MEASUREMENT OF ENVIRONMENTAL STABILITY

In order to do this, I had to be able to measure the environmental stability of my study sites. The definition and measurement of stability is perhaps the biggest difficulty encountered in examining the influence of environmental stability on community structure, in both streams and elsewhere. Low environmental stability is generally associated with increased disturbances, however, disturbances can differ in frequency (number of disturbances per unit time), intensity (physical force of the event per unit time) and/or the area affected by a particular disturbance. To what then does increased disturbance refer; increases in frequency, intensity and/or the affected area of a disturbance? The effect of each of these components of disturbance on community structure is likely to differ, and may also be different depending on the particular community involved (Miller, 1982; Pickett & White, 1985; Petraitis *et al.*, 1989). In fact the meaning of the terms disturbance, disturbance frequency and disturbance intensity are themselves often not very clear (White & Pickett, 1985). For the purposes of this study I adopted the definitions proposed by White & Pickett (1985), that a disturbance is "... any relatively discrete event in time that disrupts ecosystem, community, or population

structure and changes resources, substrate availability or the physical environment ". Similarly, frequency and intensity of disturbance, are used as defined by White & Pickett (1985) to mean the number of disturbance events per unit time, and the physical force of the event per unit area per unit time, respectively.

In their review of disturbances in lotic systems, Resh *et al.* (1988) refined this definition to include only those events outside a predictable range of environmental variability. This introduces another component of a disturbance, namely its predictability. They considered that predictability must be included in the definition of disturbance because organisms may well be adapted to withstand predictable seasonal fluctuations (although they admit the generality of this contention needs further investigation), and therefore do not represent disturbances to the organisms concerned. In my opinion, environmental stability is related to the area, frequency and/or intensity of disturbances, irrespective of how predictable they may be. For example, the most unstable site included in my study had spates (i.e., disturbances) in most months, and on this time scale, the occurrence of these spates can be considered highly predictable. However, they still resulted in the tumbling of stones and the loss of animals and periphyton. Does this mean a spate in this stream is not a disturbance because it is predictable in time or does it mean that it is a disturbance because these animals have not adapted to it? To the animals displaced or killed, a spate is surely a disturbance, despite its predictability.

It is all very well to define stability and disturbance, but actually measuring them in the field is another matter. The principal aim of my study was to compare the benthic community structure of streams differing in environmental stability. To achieve this it was therefore necessary for me to measure environmental stability objectively. Having defined a disturbance as anything "... that disrupts ecosystem, community, or population structure and changes resources, substrate availability or the physical environment " it was necessary to know *a priori* whether changes in any given variable were likely to affect ecosystem, community or population structure. Unfortunately, although the effects of some environmental variables (e.g., discharge) are relatively clear, this is not always the case.

Increases in discharge have been shown to affect invertebrate communities (Siegfried & Knight, 1977; Fisher *et al.*, 1982; McElravy *et al.*, 1989; Sagar, 1986; Scrimgeour & Winterbourn, 1989), probably by inducing substrate movement, and therefore substrate stability would seem one obvious measure of environmental stability. However, stone movement may be the result of many small disturbances (increased frequency) or a single large disturbance (increased intensity), its measurement is therefore a measure of environmental constancy not the frequency or intensity of discrete disturbance events. It is also well known that

variations in water temperature influence aquatic invertebrate life histories, metabolism and growth (Sweeney, 1978; Vannote & Sweeney, 1980) and temperature range has been used as a measure of environmental stability in a number of North American studies (e.g., Stanford & Ward, 1983). However, temperature range is also a measure of the constancy of an environmental variable not the frequency or intensity of it's effect.

Substrate movement and temperature variability almost certainly affect benthic invertebrates although probably in different ways, however, neither is discretely associated with either disturbance frequency or intensity. In order to measure environmental stability at my study sites it was therefore necessary to measure changes in environmental variables rather than the intensity or frequency of discrete disturbance events. It was also necessary to measure several such variables as no single variable can provide an all encompassing or consistent measure of stability. I therefore measured six variables to assess environmental stability; substrate movement, the Pfankuch stability index, variation in depth, variation in current speed, temperature range and stream reach tractive force (see Chapter 2 for details).

SPECIFIC AIMS

In addressing my overall objective to investigate the effect of environmental stability on benthic community structure I examined a number of aspects of benthic community structure.

Specific questions addressed in this thesis are:

1) Does environmental stability affect the food base of the communities and if so how?

2) How does environmental stability affect diversity (both species richness and evenness)?

3) Are the species-abundance distributions of these communities related to environmental stability?

4) Do communities in unstable habitats have lower persistence than communities in stable habitats?

5) Do communities in habitats of lower stability have higher theoretical resilience; measured using the local stability criteria of their community matrices?

6) If some communities are more resilient than others what community characteristics (e.g., complexity) may account for this?

7) Do theoretical measures of resilience correspond to the actual abilities of these communities to recover from disturbances?

8) Are changes in resource utilization patterns found with increasing environmental stability, and if so could they be the result of competition?

9) Could the observed communities have been created by random colonisation from the available species pool, and could random colonisation also explain recolonisation patterns following disturbances?

10) Does food web structure in these streams conform to patterns recorded for communities in a wide range of other habitats?

11) Does environmental stability affect food web structure?

CHAPTER 2

STUDY AREA

INTRODUCTION

All study sites are small water bodies that eventually flow into the Waimakariri River, in the Cass-Craigieburn region of the Southern Alps, New Zealand (Fig. 2.1).

THE CASS-CRAIGIEBURN REGION

Physical Description

The Waimakariri River catchment was formed when fault movement raised the Southern Alps during the late Tertiary and early Pleistocene, 20 million - 1 million years ago (Hayward, 1974). Late in this period, severe ice action gouged the major faults into river channels giving the catchment its basic shape. This was subsequently modified by the action of five successive glacial advances, each of which cut the valleys a little deeper. Each time they withdrew, they exposed steep greywacke (hard grey sandstone) and argillite (dark grey mudstone) mountain slopes to the wind, rain and frost. The resulting shattered rock fragments then either moved downslope to accumulate as screes, or were regrouped by the rivers into alluvial fans and terraces.

Soils were formed as the mountain slopes eroded, allowing the establishment of plants, initially on the more stable slopes, but later in the steeper areas. By the time Polynesians occupied Canterbury, forest (beech in the upper reaches merging with podocarp and broadleaf on the eastern foothills) covered most of the land below 1,200-1,400 m, with scrub and grassland above (Burrows, 1960; Moar & Lintott, 1977). Following human occupation, this vegetation suffered at the hands of both Polynesians and Europeans through fire, grazing and the introduction of exotic plants (Relph, 1958; Molloy, 1969). These events in combination with earthquakes and the repetitive freeze-thaw cycle (daily temperature extremes from below freezing to above 30°C during summer) led to a continuing period of erosion and scree formation with beech forests being replaced, except in small patches, by secondary scrub and tussock (Relph, 1957; Burrows, 1960). More detailed information on the geology, geography and flora of the region can be found in Burrows (1977).

Climate

Macro-climate in the area is characterised by high summer temperatures, relatively mild winters (given the altitude and latitude) and 1,250-3,980 mm annual rainfall,

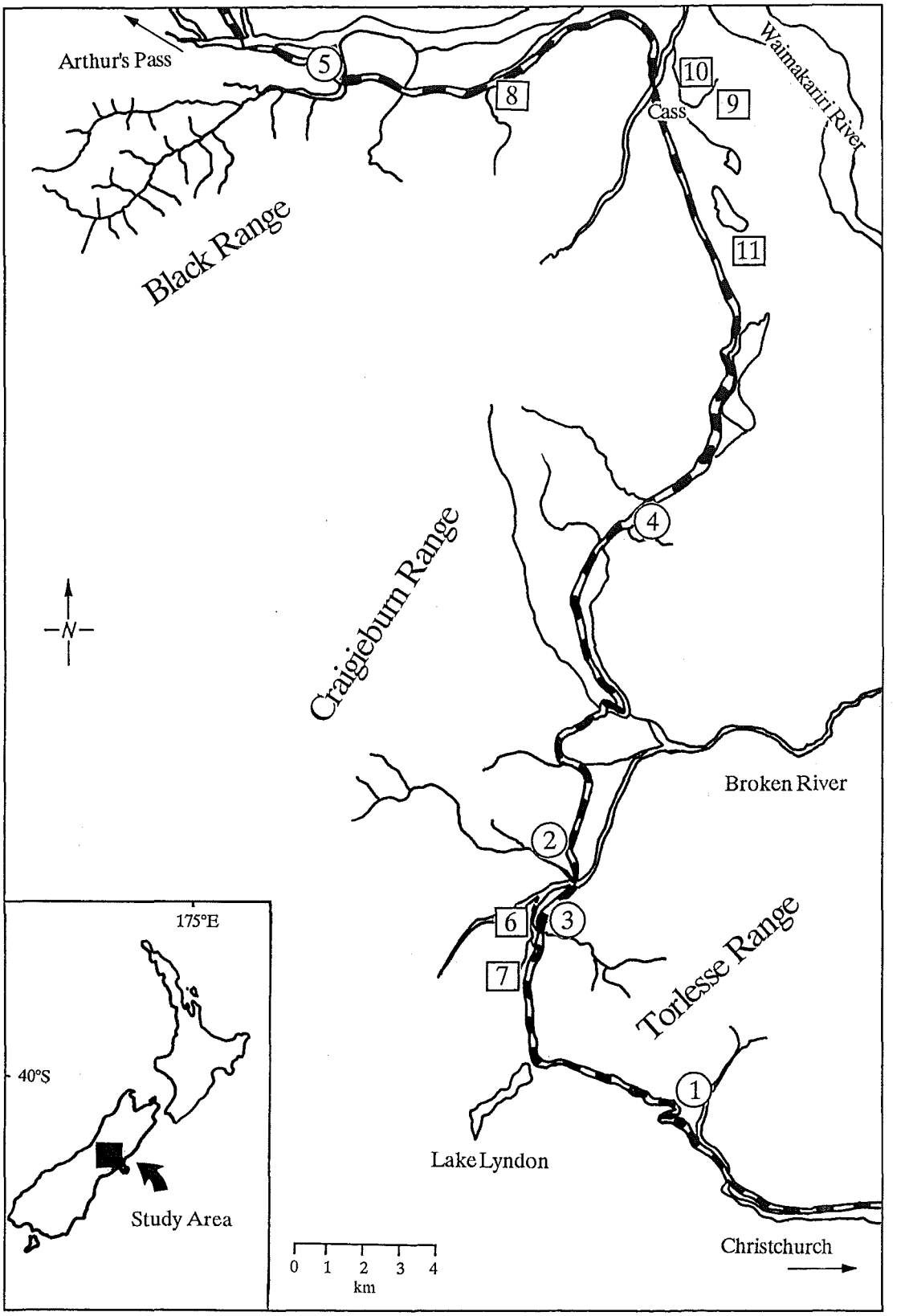


Figure 2.1. Location of the study sites in the Waimakariri River basin. The unstable sites are: Kowai River = 1; Whitewater Stream = 2; Dry Stream = 3; Craigieburn Cutting Stream = 4 and Bruce Stream = 5. The stable sites are: Porter River = 6; Slip Spring = 7; Cora Lynn Stream = 8; Middle Bush Stream = 9; Grasmere Stream = 10 and Lake Grasmere = 11.

distributed relatively evenly throughout the year (Greenland, 1977). Air temperature at the Craigieburn Forest Meteorological Station, for 1964-1980, ranged from -9.6°C to 32.9°C, with a mean of 8°C for the same period (New Zealand Meteorological Service, 1983). The monthly range at the Cass Field Station over the study period (June 1987 - June 1989) is given in Fig. 2.2. Snow falls on a few occasions in most winters, but seldom persists for more than a few days at any of the study sites. The catchment exhibits a wide range in annual rainfall from east to west, with annual precipitation at Arthur's Pass, 10 km west of Bruce Stream (the most westerly site), five times greater than the annual mean (100 cm) at Kowai River (the most easterly site) (Greenland, 1977). Consequently, there can be marked differences in micro-climate between individual valley basins. Rainfall records for the study period, from climate stations closest to each of the three main valleys are given in Fig. 2.3.

THE STUDY SITES

Introduction

Study sites were chosen to represent a range of streams (small, large, forested, and open) that would differ primarily with respect to the variability of their physical

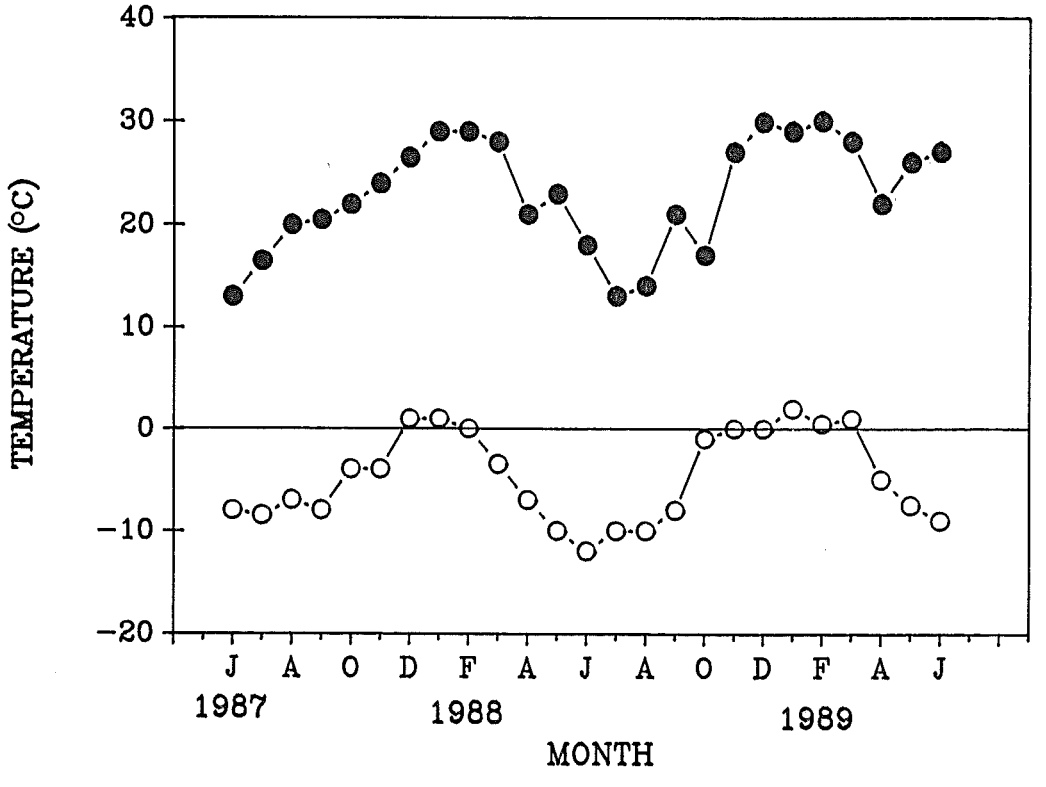


Figure 2.2. Monthly maximum and minimum air temperatures recorded at the Cass Biological Station from June 1987 to June 1989.

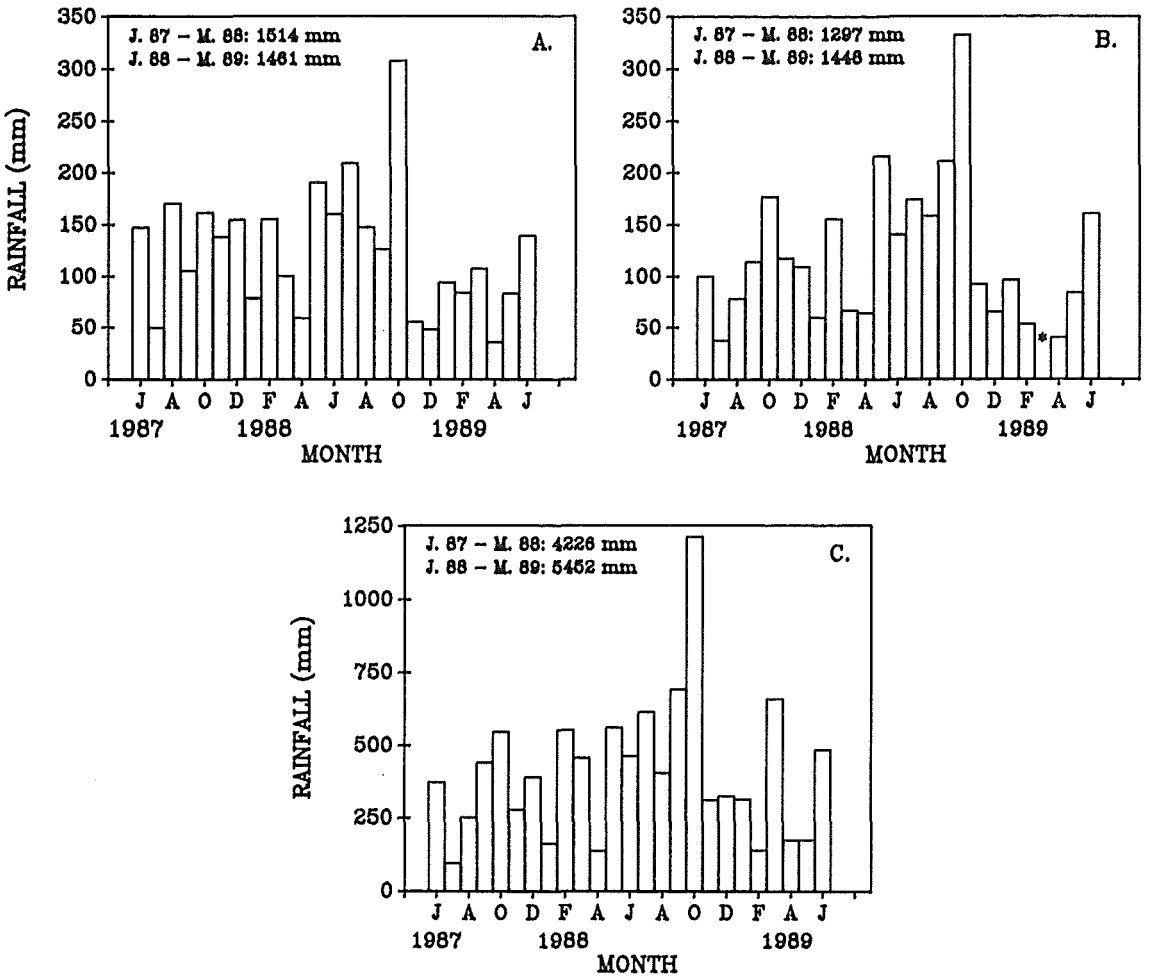


Figure 2.3. Monthly rainfall records between June 1987 and June 1989. A. Craigieburn Forest Park (altitude = 914 m a.s.l) (data courtesy T. McSeveny, Forest Research Institute), B. Chilton Valley, Cass (altitude = 780 m a.s.l.) (data courtesy A. Sturman, University of Canterbury), C. Arthur's Pass (altitude = 738 m a.s.l.) (data courtesy M. Davies, Department of Conservation) (* - data missing).

characteristics. This meant that initially, streams were categorised as "stable" or "unstable" based on the nature of their sources. Those that arose from either a spring or lake outlet were reasoned to be relatively stable, whereas streams without any such point source were reasoned to be comparatively unstable. The stony, wave-washed, southwestern end of Lake Grasmere was also included in the study because it appeared to be a stable environment that superficially resembled a stream, and has a fauna similar to that of streams in the region (Stout, 1977). The altitude and location of each of the study sites is given in Table 2.1.

Unstable Sites

Kowai River (Plate 2.1)

A second order braided stream occupying a 100 m wide flood plain, it drains a catchment of predominantly subalpine tussock scrub, bare scree, and remnant patches of mountain beech (*Nothofagus solandri* var. *cliffortioides*). The position of

Table 2.1. Map location and altitude of the study sites.

SITES	Location	Altitude (m)
UNSTABLE		
Kowai River	43°19'S, 171°47'E	610
Whitewater Stream	43°14'S, 171°43'E	730
Dry Stream	43°16'S, 171°43'E	790
Craigieburn Cutting Stream	43°09'S, 171°45'E	760
Bruce Stream	43°02'S, 171°38'E	640
STABLE		
Porter River	43°16'S, 171°43'E	790
Slip Spring	43°16'S, 171°42'E	790
Cora Lynn Stream	43°02'S, 171°41'E	610
Middle Bush Stream	43°02'S, 171°46'E	610
Grasmere Stream	43°02'S, 171°46'E	580
Lake Grasmere	43°05'S, 171°45'E	580

the channel at this study site changed repeatedly during the course of the study, moving distances of up to 5 m in the one month interval between visits to the site.

Whitewater Stream (Plate 2.2)

A third order braided stream occupying a 40 m wide flood plain, it drains a catchment of predominantly tussock scrub which is grazed by sheep and cattle for much of the year. The stream channel moved once during the course of the study, the original two channels merging into one and shifting 20 m as a result of a major spate in September 1988.

Dry Stream (Plate 2.3)

A small second order stream occupying a 50 m wide flood plain. Dry stream also drains a catchment of predominantly subalpine tussock scrub, bare scree, and remnant patches of mountain beech. The site dried up periodically during both summers of the study (December-April). The channel changed position once during the study, moving to a new position 5 m from the original after a spate in July 1988.

Craigieburn Cutting Stream (Plate 2.4)

A first order stream draining a catchment of mainly subalpine scrub and scree, but with a 13 ha remnant stand of mountain beech through which the stream flows at

Plate 2.1. Kowai River

Plate 2.2. Whitewater Stream

Plate 2.3. Dry Stream

the study site. The stream here has a fairly complete canopy, is well shaded, and receives comparatively high allochthonous inputs from the overhanging vegetation (Rounick & Winterbourn, 1983a). Debris dams and pools were present but sparse, and changed position considerably during the course of the study.

Bruce Stream (Plate 2.5)

A third order braided stream occupying a 100 m wide flood plain, it drains a catchment of predominantly mountain beech and several stands of Monterey pine (*Pinus radiata*). Channel position changed radically and regularly during the course of the study, moving distances of up to 20 m laterally on at least one occasion.

Plate 2.4. Craigieburn Cutting Stream

Plate 2.5. Bruce Stream

Stable Sites

Slip Spring (Plate 2.6)
This site is the rheocrene/holocrene spring source of the Porter River, arising at the base of a large scree and flowing through tussock grassland before flowing into Porter River. The springbrook is colonised by extensive growths of *Myriophyllum* sp. and *Callitriche stagnalis*, both of which are periodically grazed by cattle. Because of this, sampling sites did not include weed beds.

Porter River (Plate 2.7)
An un-named, second order tributary of the Porter River proper, fed by two rheocrene/holocrene springs, one of which is Slip Spring. It runs through tussock grassland for its entire (1.6 km) length.

Cora Lynn Stream (Plate 2.8)
A first order, spring-fed stream draining a catchment of predominantly matagouri (*Discaria toumatou*) and tussock scrub. The stream runs through tussock grassland at the study site but passes through thick matagouri scrub just prior to this.

Middle Bush Stream (Plate 2.9)
The other forested site in the study, this stream is located in the Cass Basin. It is a first order stream that drains a 28 ha catchment of subalpine scrub, tussock and bare scree. The stream has a rheocrene spring source and enters a 3-4 ha stand of mountain beech within which the study site was located. Below the forest it usually flows underground before discharging into Grasmere Stream. Middle Bush Stream is well shaded and its bed consists of alternating pools (caused by log debris dams) and riffles. Forest litter enters the stream year round with a maximum in the summer half of the year (Winterbourn, 1976). Sampling was confined to riffles.

Grasmere Stream (Plate 2.10)
The outlet of Lakes Sarah and Grasmere, this stream flows through tussock grassland for much of its length but passes through a bed of *Phormium tenax* and *Typha orientalis* just before the study site.

Lake Grasmere (Plate 2.11)
One of five small lakes in the Cass region, Lake Grasmere was dammed by morainic ice-eroded rock and postglacial fan-building during the Poulter glacial

Plate 2.6. Slip Spring

Plate 2.7. Porter River

Plate 2.8. Cora Lynn Stream

Plate 2.9. Middle Bush Stream

Plate 2.10. Grasmere Stream

Plate 2.11. Lake Grasmere

advance, about 16,000-13,000 years before present (Gage, 1959, 1977). A 63 ha lake, its 1,850 ha catchment is primarily tussock grassland, 50% of which is used for agriculture (Gibson, 1978). At the stony, southwestern end of Grasmere, the lake is exposed to extensive wind-induced wave action. The study site was a 20 m stretch of this exposed shore which also receives water from numerous small springs.

PHYSICOCHEMICAL CHARACTERISTICS

Introduction

A number of physical and chemical parameters were measured at each site during the course of the study in order to investigate differences between the "stable" and "unstable" site groups. This was done to establish whether the two groups of streams differed with respect to various physicochemical characteristics and/or the stability (i.e., variability) of these characteristics.

Materials and Methods

Physical characteristics

Spot records of depth and current speed were obtained monthly between October 1987 and May 1989. Measurements were made near the centre of the stream at a marked point, so that temporal variability could also be assessed. This was achieved by calculating the absolute difference between the measurement in one month and that in the preceding month for all recorded months. Current speed was measured with a Pygmy Gurley current meter, or by recording the time taken for a cork to travel 2 m when the meter failed to function, or flow was too low for it to operate.

A comparative estimate of discharge at each of the study sites was made in November 1989. This was calculated by measuring current speed with a Pygmy Gurley current meter, midway between the surface and the stream bed, and multiplying this by the stream cross-sectional area. Slope was measured by recording the fall in height along a 20 m section of stream, with an Abney level.

Maximum-minimum and/or spot water temperatures were recorded monthly between October 1987 and May 1989. However, the number of recordings made varied considerably between sites. This was because maximum-minimum thermometers were frequently buried or washed away at the more unstable sites, and in May 1988 I gave up using them at Kowai River and Bruce Stream.

The particle size distribution of stream bed materials at each site was estimated

by measuring the three main axes of 100 randomly selected stones (i.e. particles greater than 0.5 cm) from each stream (Newbury, 1984). Half the stones were collected from randomly assigned, grided 0.5 m^2 quadrats (the stones were collected from the intersection points of the 10 cm^2 grids) and the other half with a cross-sectional transect. Mean particle size, geometric mean particle size and geometric variance were calculated for bed materials at each site (Shirazi & Seim, 1979).

Chemical characteristics

Conductivity and pH of water samples were recorded approximately monthly between January 1988 and May 1989. Samples were collected in opaque, polyethylene bottles and stored in the dark at 5°C until analysis could be undertaken (this was always within 24 hours). Conductivity was measured with a Radiometer CDM 2e conductivity meter and recordings were converted to equivalent values at 25°C using the appropriate conversion factor (Golterman, 1970). Water pH was measured with a Metrohm 632 pH meter.

Alkalinity of water samples was measured between February and November 1989 (five samples covering each of the seasons) as described by Mackereth (1963).

Concentrations of nitrate-nitrogen (NO_3-N) in water samples collected in March 1988 and November 1989 were measured with the cadmium reduction alpha-napthylamine-sulfanilic acid technique using the Hach Chemical Company reagent NitraVer V (accurate to 0.5 mg l^{-1}). Absorbances were measured on a Kontron Spectrophotometer at 525 nm and converted to nitrate-nitrogen concentrations using a standard curve.

Pfankuch stability index

The stability of each stream was evaluated using the stream reach inventory and channel stability evaluation technique of Pfankuch (1975). This is based on hydrologic aspects of the channel and streambank, and is essentially a hydrological engineers tool used for assessing the stability of 2nd to 4th order, forested mountain streams in the U.S.A. Eifert & Wesche (1982) found it was a useful technique for evaluating the suitability of habitat for salmonid populations in the U.S.A. and the procedure has been used to assess stream bed stability in a number of studies in New Zealand (e.g., Rounick & Winterbourn, 1982; Winterbourn & Collier, 1987; Graesser, 1988), and overseas (Trotter, 1990).

The technique involves rating fifteen variables in three regions of the stream channel - the upper banks, lower banks and stream bottom according to predetermined weightings given on the evaluation form (see Rounick & Winterbourn,

1982). These are summed to give an overall index that evaluates "... the resistive capacity of mountain stream channels to the detachment of bed and bank materials and to provide information about the capacity of streams to adjust and recover from potential changes in flow and/or increases in sediment production... " (Pfankuch, 1975). The index ranges from a low of 52 (most stable) to a high of 152 (least stable). Because of the subjective nature of the assessments that make up the index, four people (including myself), all of whom had used the index before, rated each of the study sites. The results were then averaged.

Substrate movement

Although the Pfankuch stability index has been used previously in studies of debris retention (Trotter, 1990), invertebrate community structure (e.g., Rounick & Winterbourn, 1982; Winterbourn & Collier, 1987; Graesser, 1988), and to characterise fish habitat (Eifert & Wesche, 1982), it measures environmental stability on a relatively coarse scale (i.e., the stream reach) which is unlikely to be directly relevant to stream invertebrates. Although this problem may be partly circumvented by only using the third of the index related to the actual stream bed (i.e., the bottom component), this still relies on a "one-off", somewhat subjective assessment of stream bed stability. A direct measurement of actual substrate movement, the scale at which forces affecting invertebrate community dynamics are most likely to be acting, should therefore be more appropriate.

I obtained such a measure by recording the movement of marked stones within the stream bed. Five fluorescently painted stones in each of three size classes (small < 55 mm; medium 55-90 mm; large, 90-180 mm longest diameter) were placed at a marked point in the stream. Every month between December 1987 and May 1989 the distance travelled by each of the stones was recorded. To convert these data to a single measure of stream substrate movement, the distance travelled by each stone was multiplied by the mean weight of stones in that size class and summed for all stones at that site. On any occasion that a stone was not recovered, an arbitrary distance of 50 m was assigned to the distance travelled, as this was the maximum distance at which a stone was recovered. The value obtained was then converted to a percentage scale, by dividing the actual measure by the maximum possible score (i.e., 405.5 kg m, achieved if all stones disappeared), so that 0 = no stones moved and 100 = all stones disappeared. Each month, all stones were returned to the starting point or replaced if they had disappeared.

Measurement of tractive force

Although the above technique does measure actual substrate movement, it is really only measuring it in a small area of the stream bed (i.e., where the stones are placed

and/or move to). However, it is possible to calculate the theoretical proportion of particles that should be moving in uniform flow conditions within the entire stream reach by calculating the streams tractive force.

A column of moving water exerts a force on the stream bed parallel to the slope of the channel, such that if it exceeds a critical value it will set substrate material and organisms in motion. The tractive force of a stream reach T, can be related to the specific weight of water (1000 kg m^{-3}), depth of flow D (m), and the slope of the stream channel S, so that T = 1000.D.S (kg m^{-2}) (Newbury, 1984).

The critical tractive force (that at the point of incipient motion) for rounded, noncohesive particles > 0.5 cm diameter is approximately equal to the diameter of the particle (cm) (Lane, 1955). Given the particle size distribution of a stream reach it is therefore possible to calculate what proportion of the particles should be moving in uniform flow conditions at a given depth. The tractive force for each of the study reaches was measured, and using the particle size distribution data collected as described above, the percentage of substrate predicted to be moving at any point in time was calculated.

Analysis

To assess whether the two groups of streams were different with respect to individual physicochemical parameters and/or stability measures, all measured variables were analysed with a three level mixed model (factor A & B fixed, factor C random) analysis of variance (ANOVA) using SAS (1985). For the analysis of physical parameters the streams were treated as nested effects, however, for all subsequent analyses the streams were grouped together based on their size, geographic location and whether they were open or forested. To investigate differences based on a number of these variables together, multiple analysis of variance (MANOVA), cluster analysis (using Euclidean distance measures and a group average clustering algorithm), and principal components analysis (PCA) were employed. MANOVA was carried out with SAS (1985), whereas PCA and cluster analysis were carried out with the PC-ORD multivariate statistics package (McCune, 1987).

Results

Physical characteristics

A summary of the physical characteristics of each site is given in Table 2.2 along with the results of analysis of variance tests for differences in these characteristics between the site groups. Discharge, slope and temperature were not significantly

Table 2.2. Physical characteristics of study sites (mean values with the range below in parentheses). F values testing the null hypothesis that stable and unstable sites were similar with respect to these variables are also given. NA = not applicable.

SITES	Depth (cm)	Current (cm s^{-1})	Discharge (l s^{-1})	Width (m)	Slope (°)	Temperature (°C)
UNSTABLE						
Kowai River	29 (17-43)	103 (34-161)	1069	5.3 (4.0-6.7)	2.7 (2-3)	13.0 (2.5-31)
Whitewater Stream	16 (6-25)	75 (37-125)	617	5.8 (2.5-8.9)	3 (2-4)	10.4 (1-21)
Dry Stream	9 (0-19)	44 (0-90)	33	1.9 (1.7-2.1)	2 (1-3)	10.0 (0-27)
Craigieburn Cutting Stream	8 (4-15)	40 (15-87)	7	1.1 (0.8-1.6)	8.3 (4-13)	8.9 (2.5-23)
Bruce Stream	34 (13-60)	94 (44-143)	1915	6.3 (5.5-7.1)	2 (1-3)	8.8 (1-18)
STABLE						
Porter River	21 (17-26)	90 (54-137)	422	4.9 (3.8-5.7)	2 (2-2)	9.0 (6-11)
Slip Spring	9 (6-12.5)	46 (21-92)	154	2.5 (1.5-3.7)	6.3 (2-13)	8.1 (7.5-9)
Cora Lynn Stream	11 (0-24)	37 (0-75)	21	1.3 (0.8-1.6)	2.5 (1-5)	8.6 (3-13)
Middle Bush Stream	5 (0-12)	36 (19-70)	3	0.9 (0.4-1.3)	7 (3-10)	8.0 (1.5-15)
Grasmere Stream	29 (19-45)	85 (28-127)	254	3.4 (2.8-3.9)	2 (2-2)	11.7 (2.5-22.5)
Lake Grasmere	29 (14-53)	NA	NA	NA	NA	13.0 (5-23.5)
F value	0.49	10.86	0.63	24.24	0.02	1.13
Degrees of Freedom	1,18	1,17	1,8	1,43	1,24	1,18
Significance	n.s.	**	n.s.	***	n.s.	n.s.

different between the stable and unstable streams. However, depth, current and width were significantly different between the two groups. The magnitude of these differences was relatively small, however; mean depth differed by only 2 cm between the two groups (17 and 19 cm for stable and unstable groups, respectively), mean current speed by 12 cm s^{-1} (59 and 71 cm s^{-1}, respectively) and width by 1.48 m (2.6 and 4.08 m, respectively). As depth and current were assessed by monthly spot measurements at the same point in the stream, the observed differences were probably smaller than those that actually exist within each study site. Differences in width reflect a difference in the nature of the two types of stream; the unstable sites were predominantly on braided streams that meandered over broad gravel beds, whereas the stable sites were on more defined, single thread channels.

Substrate characteristics of the study sites are given in Table 2.3. All of the sites were remarkably similar in this respect, with mean particle size between 4.7 and 8.5 cm. None of the substrate parameters were significantly different between the two groups of streams.

Overall differences between stable and unstable stream groups, based on all the physical variables (standardised to a mean of 0 and a standard deviation of 1) were non significant (Wilks' Lambda = 0.01, F = 23.44, df = 8,1, $P > 0.05$).

Chemical characteristics

A summary of chemical characteristics of the study sites is given in Table 2.4. All sites had circumneutral pH (means between 7.2 and 8.0) and moderate conductivities, although some high values were recorded at a few sites during very low summer flows. Conductivity and pH were not significantly different between the stable and unstable site groups. Alkalinity however, was significantly different between the two groups, although only at the 5% level (means of 31 and 20 mg $CaCO_3$ l^{-1} for stable and unstable site groups, respectively). Nitrate-nitrogen (NO_3-N) concentrations at all the sites were below detectable levels (< 0.5 mg l^{-1}). Reactive phosphorus (PO_4-P) concentrations at a number of these sites, were also found to

Table 2.3. Substrate characteristics of the study sites. F values testing the null hypothesis that stable and unstable sites are similar with respect to these variables are also given.

SITES	Mean particle size (cm)	Geometric mean particle size (cm)	Geometric variance (cm)	Maximum particle size (cm)
UNSTABLE				
Kowai River	7.4	6.2	1.9	32
Whitewater Stream	7.8	6.3	2.3	37
Dry Stream	5.4	4.2	2.1	31
Craigieburn Cutting Stream	8.1	4.6	2.2	83
Bruce Stream	7.4	6.0	2.0	30
STABLE				
Porter River	6.6	6.1	1.9	24.5
Slip Spring	8.5	6.4	2.4	47
Cora Lynn Stream	7.2	5.5	2.0	53
Middle Bush Stream	6.4	4.9	2.3	30
Grasmere Stream	4.7	4.3	1.7	21
Lake Grasmere	5.7	4.7	1.7	23
F values	0.89	0.06	0.47	0.74
Degrees of freedom	1,9	1,9	1,9	1,9
Significance	n.s.	n.s.	n.s.	n.s.

Table 2.4. Chemical characteristics of the study sites (mean values with the range below in parentheses; conductivity values are medians). F values testing the null hypothesis that stable and unstable sites were similar with respect to these variables are also given.

SITES	pH	Conductivity $\mu s\ cm^{-1}$	Alkalinity (mg $CaCO_3\ l^{-1}$)
UNSTABLE			
Kowai River	7.7	69	17.8
	(6.4-8.5)	(31-138)	(12-21)
Whitewater Stream	7.5	53	17.6
	(6.6-8.1)	(29-69)	(10-20)
Dry Stream	7.6	49	18.4
	(6.9-8.1)	(29-50)	(18-19)
Craigieburn Cutting	7.3	53	17.7
Stream	(6.6-7.9)	(19-61)	(12-22)
Bruce Stream	7.4	72	26.1
	(6.6-7.9)	(55-96)	(17-32)
STABLE			
Porter River	7.5	55	20.3
	(6.6-8.1)	(38-62)	(11-24)
Slip Spring	7.2	41	22.2
	(6.6-8.0)	(41-97)	(11-26)
Cora Lynn Stream	7.6	131	41.6
	(6.6-8.0)	(100-140)	(32-47)
Middle Bush Stream	7.8	110	35.0
	(7.1-8.3)	(61-121)	(19-48)
Grasmere Stream	7.4	83	33.2
	(6.7-8.2)	(57-95)	(17-47)
Lake Grasmere	8.0	85	32.2
	(7.0-9.0)	(61-101)	(18-39)
F value	0.06	3.95	13.86
Degrees of Freedom	1,12	1,12	1,4
Significance	n.s.	n.s	*

be below detectable levels (< 0.04 mg l^{-1}) in a previous study (Winterbourn & Fegley, 1989).

No overall differences were found between the two groups of streams based on these chemical parameters (standardised to a mean of 0 and a standard deviation of 1) (Wilks' Lambda = 0.45, $F = 2.80$, $df = 3,7$, $P > 0.05$).

Overall physicochemical differences

Cluster analysis of all chemical and physical parameters (standardised by a norm

transformation), including stream order and the nature of the stream canopy (Fig. 2.4), split the sites into two principal groups, reflecting a division between small and large streams, rather than stable and unstable ones. Streams in the "large" group were all open streams between 3 and 6 m wide, 16-34 cm deep, and with mean current velocities between 75 and 102 cm s^{-1}. In contrast, the "small" group comprised streams between 0.9 and 2.5 m wide, 5-11 cm deep, and with mean current speeds of 36-46 cm s^{-1}. The latter group also included the lake, probably because many of the variables, such as current speed, could not be measured there. Differences between sites with regard to their overall physicochemical characteristics therefore appeared to be related more to the size and location of the site than its perceived stability.

Variability in physical characteristics

Average differences in spot measurements of depth and current speed at each site in consecutive months are given in Table 2.5. Mean differences in depth ranged from 3 cm at Craigieburn Cutting to 19 cm at Bruce Stream (unstable sites), and from 2 cm at Slip Spring to 7 cm at Lake Grasmere (stable sites). Mean differences in current speed ranged from 18 cm s^{-1} at Craigieburn Cutting to 46 cm s^{-1} at Bruce Stream (unstable sites), and from 11 cm s^{-1} at Middle Bush Stream to 34 cm s^{-1} at Grasmere Stream (stable sites). Both parameters were significantly greater for the unstable site group.

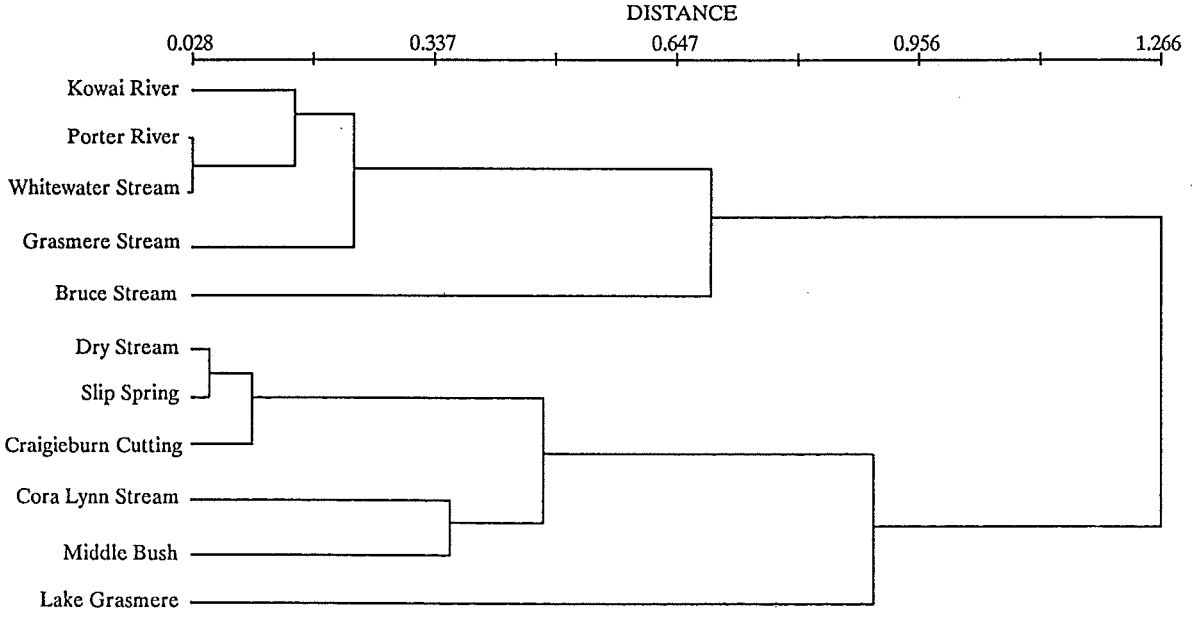


Figure 2.4. Cluster analysis of mean physicochemical characteristics for each of the study sites. Data were standardised with a norm transformation and the dendrogram constructed using Euclidean distance and a group average clustering algorithm.

Table 2.5. Mean monthly variation in depth, current velocity and temperature for the study sites (ranges for these measures are given below in parentheses). F values testing the null hypothesis that stable and unstable sites have similar variation in these factors are also given. NA = not applicable.

SITES	Monthly Variation of Depth (cm)	Monthly Variation of Current (cm s^{-1})	Monthly Temperature Range (°C)
UNSTABLE			
Kowai River	7	44	9.8
	(0.5-21)	(10-99)	(3.5-24)
Whitewater Stream	4	27	9.8
	(0-14)	(0-69)	(5.5-14)
Dry Stream	6	35	9.8
	(0-15)	(0-81)	(6-18)
Craigieburn Cutting	3	18	5.8
Stream	(0-8)	(0-67)	(0.5-13.5)
Bruce Stream	19	46	9.4
	(1-42)	(1-100)	(7-12)
STABLE			
Porter River	3	29	2.2
	(0-7)	(3-83)	(1-4)
Slip Spring	2	18	0.5
	(0-6)	(1-43)	(0-3)
Cora Lynn Stream	4	13	2.5
	(0-12)	(0-41)	(1-5)
Middle Bush Stream	3	11	5.7
	(0-10)	(0-49)	(4-8.5)
Grasmere Stream	4	34	6.3
	(0-15)	(1-78)	(3.5-12)
Lake Grasmere	7	NA	8.4
	(0-20)		(1-13)
F value	29.70	12.81	70.40
Degrees of freedom	1,17	1,16	1,17
Significance	***	***	***

Mean monthly temperature range is also given in Table 2.5. It was between 5.8°C and 9.8°C at the unstable sites and 0.5°C and 8.4°C at the stable sites. Temperature range was also significantly greater at the unstable sites.

Pfankuch stability index

Total Pfankuch stability index scores and subscores for the three channel compo-

nents are given in Table 2.6. Total index scores ranged from a high of 122 at Kowai River to a low of 64 at Slip Spring. All four measurements were significantly higher for the streams in the unstable site group than those in the stable site group.

Substrate movement

Distances moved by stones at each of the sites are plotted in Fig 2.5. There appeared to be a good relationship between these measures and my observations of high discharge events. Two spates in May and September 1988 (corresponding to the Greymouth flood events), caused major physical changes at several of the sites and these stand out clearly in the monthly plots. Overall, the stable sites had little or no substrate movement. However, the two most unstable sites (Kowai River and Bruce Stream) had all the stones disappear in most months, and the other unstable sites had intermediate levels of substrate movement, which occurred principally in the winter months (May - September).

Mean movement values are summarized in Table 2.7 and ranged from 0 at Slip Spring (where there was no recorded stone movement) to 97 at Bruce Stream (where all stones disappeared in most months). Again the unstable sites had significantly higher measures than the stable sites.

Table 2.6. Pfankuch stability index scores with F values testing the null hypothesis that these scores were similar for stable and unstable sites.

SITES	Total	Upper Bank component	Lower Bank component	Bottom component
UNSTABLE				
Kowai River	122.25	36.5	36	49.75
Whitewater Stream	110.25	34	37.75	38.5
Dry Stream	106.25	29.5	33.75	42
Craigieburn Cutting Stream	108.25	30	34	44.25
Bruce Stream	115.75	26.75	39	50
STABLE				
Porter River	70.25	17.75	21.5	31
Slip Spring	64	16	17	31
Cora Lynn Stream	68.25	13.75	24	30.5
Middle Bush Stream	111.75	36	34	41.75
Grasmere Stream	74.25	12.75	25.75	35.75
Lake Grasmere	70.25	14	26	30.25
F value	104.39	114.76	53.24	26.11
Degrees of freedom	1,33	1,33	1,33	1,33
Significance	***	***	***	***

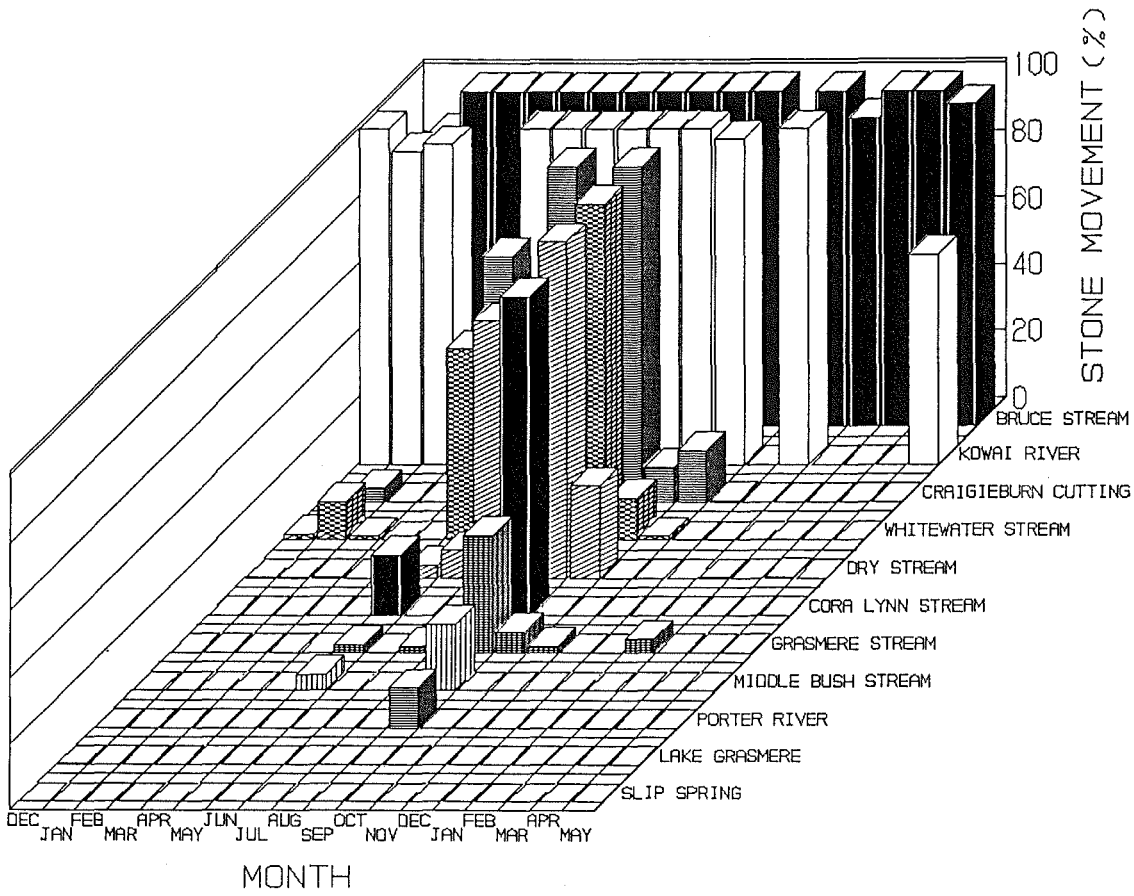


Figure 2.5. Stone movement measurements (expressed as a percentage of the maximum recordable movement) for each of the study sites between December 1987 and May 1989.

Tractive force measurements

Tractive force measurements obtained for each site, and the percentage of the substrate predicted to move at such a tractive force, are given in Table 2.7. Tractive force ranged from 2.3 to 9.1 kg m^{-2}, and between 13 and 76% of the substrate was predicted to be moving in linear flow and mean depth. Neither critical tractive force nor the percentage of substrate predicted to be moving was significantly different between the two groups of streams.

Overall stability

In general, all the stability measures were significantly correlated with each other (Table 2.8). Notable exceptions however, were the predicted substrate movement and the total Pfankuch stability scores. The former were not correlated with any other stability measures. Carson & Griffiths (1987), in their review of bedload transport in gravel channels, queried the generality of the relationship between critical tractive force and the point of incipient motion formulated by Lane (1955). They suggested the relationship may not hold for Canterbury rivers because of the large variation in hydraulic stresses that occurs in braided rivers. Neither my

Table 2.7. Mean stone movement measures, tractive force and the percentage of the substrate predicted to move given the tractive force. F values testing whether these variables were significantly different between stable and unstable groups are also given. NA = not applicable.

SITES	Stone movement measure (%)	Tractive force kg m^{-2}	Percentage of substrate moved by tractive force (%)
UNSTABLE			
Kowai River	63.79	8.09	72
Whitewater Stream	17.21	4.13	28
Dry Stream	11.98	4.10	50
Craigieburn Cutting Stream	18.59	6.07	66
Bruce Stream	96.86	9.06	70
STABLE			
Porter River	0.67	7.24	68
Slip Spring	0.00	8.65	63
Cora Lynn Stream	6.26	7.45	76
Middle Bush Stream	1.37	6.65	68
Grasmere Stream	2.97	2.30	13
Lake Grasmere	0.02	NA	NA
F value	62.80	0.01	0.00
Degrees of freedom	1,17	1,8	1,8
Significance	***	n.s.	n.s.

Table 2.8. Correlation (*r*) of mean stability measures with each other. * indicates significance at the 5% level.

STABILITY MEASURE	Depth variability	Current variability	Temperature range	Stone movement	Total Pfankuch index	Bottom component Pfankuch	Predicted substrate movement
Depth variability	1.00						
Current variability	0.75*	1.00					
Temperature range	0.56	0.66*	1.00				
Stone movement	0.94*	0.74*	0.60	1.00			
Total Pfankuch index	0.49	0.41	0.85*	0.62	1.00		
Bottom component of Pfankuch index	0.68*	0.58	0.80*	0.80*	0.92*		
Predicted substrate movement of tractive force	0.18	-0.18	-0.30	0.28	0.09	0.16	1.00

substrate movement data nor my general observations support the prediction that a high percentage of the substrate materials > 0.5 cm diameter was in fact moving at many of my study sites. It therefore appears, that in these streams at least, critical tractive force is not a very useful predictor of substrate stability.

The total Pfankuch stability scores were only correlated significantly with

temperature range, and therefore they too did not appear to reflect the overall physicochemical stability of a site. Many of the criteria used to obtain the index relate to the probability of hydrologic stability and do not necessarily measure actual variations in the environment. For example, the water level in Porter River is always just a few centimetres below bankfull, a highly unstable criterion according to the Pfankuch procedure. However, the stream is spring-fed and the flow never increases much above this level, so constancy of flow, in contrast to the index score, indicates that it is a very stable site. As I suggested in the materials and methods section, the bottom component of this index may be more appropriate at the scale of aquatic community dynamics, a suggestion supported by results reported by Winterbourn & Collier (1987). It was correlated with all but two of the other stability measures, and one of these was predicted substrate movement.

Depth variability, current variability and stone movement were all inter-correlated. Temperature range although it is unlikely to be directly linked to the other more hydrologically based stability measures, should be correlated with these measures because of overall differences in stability between the two groups of streams. The spring and lake-fed nature of the "stable" sites not only ensures a constant flow but also a relatively constant temperature regime. However, it was only correlated with current variability and both the Pfankuch index scores.

To examine the role of environmental stability in affecting community processes with each of these stability measures separately clearly would be rather confusing. Each addresses a slightly different component of a site's physical stability, and with six different variables, one could in theory reach six equally plausible conclusions about the effect of environmental stability. For example, diversity may decrease with increasing substrate movement, but increase as temperature range increases, both of which represent decreasing environmental stability. In order to obtain a single measure of a site's overall physical stability I combined all the values into a single multivariate stability score using principal components analysis. For this analysis, the Pfankuch stability score was replaced with the more appropriate bottom component of the index. The multivariate stability scores (the PCA scores for axis 1 which accounted for 61% of the variation in the six stability measurements) for all sites, are shown as a linear hierarchy in Fig. 2.6., with higher scores indicative of decreasing stability.

Cluster analysis (not shown) of all the stability measures (standardised by a norm transformation) (again replacing the Pfankuch score with its bottom component, and omitting the predicted substrate movement because it did not correspond well with the other measures) initially split the streams into two groups; Kowai River and Bruce Stream in one group, the remaining sites in the other. This was not

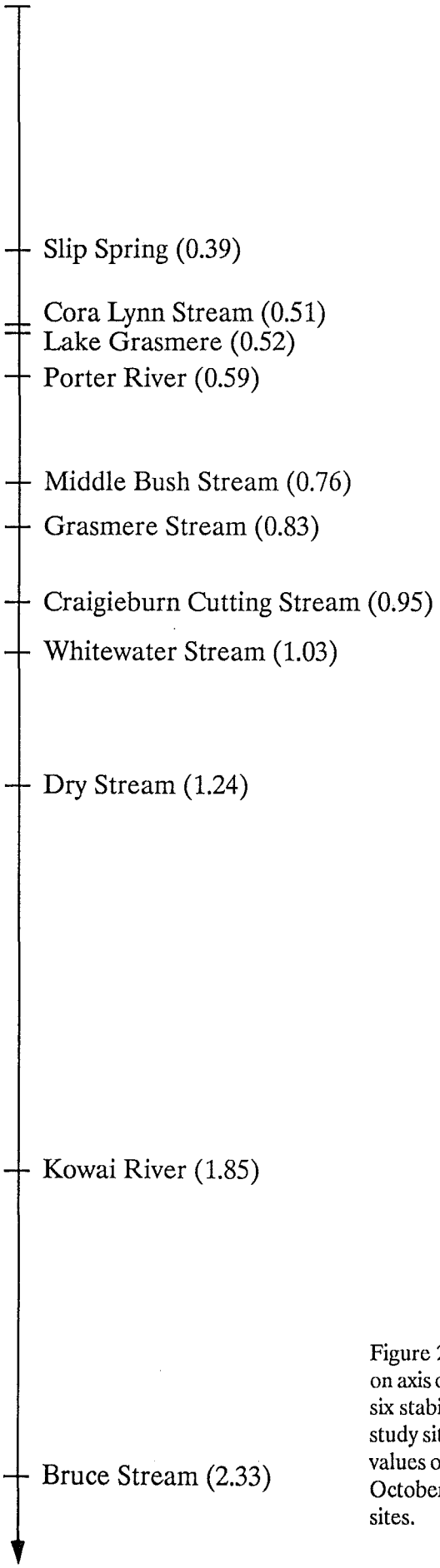


Figure 2.6. Multivariate stability scores, based on axis one of a principal components analysis of six stability measures (see text), for each of the study sites. The six stability measures are mean values of monthly measurements made between October 1987 and May 1989 at each of the study sites.

surprising, as the former two sites were by far the most unstable. If temperature range was downweighted (by 0.5) so that hydrological stability characteristics were most strongly weighted, Kowai River and Bruce Stream again formed a group of their own (Fig. 2.7), and the other sites were split into three smaller groups; the remaining unstable sites; Lake Grasmere; and the stable stream sites.

Overall differences between my initial "stable" and "unstable" site groupings were examined with MANOVA. For this analysis, the Pfankuch index was again replaced with its bottom component and the predicted substrate movement was excluded. All variables were standardised to a mean of 0 and a standard deviation of 1. With all stability measurements included, the site groups were not significantly different (Wilks' Lambda = 0.24, F = 2.57, df = 5,4, $P > 0.05$). However, if the current variability measure was excluded from the analysis the two groups were significantly different (Wilks' Lambda = 0.24, F = 4.83, df = 4,6, $P < 0.05$). Similarly, if the unstable group was split into two (one containing Kowai River and Bruce Stream, and the other containing the remaining unstable sites) all three groups, were significantly different in overall stability (Wilks' Lambda = 0.01, F = 6.88, df = 10,6, $P < 0.05$).

Summary

In summary, the study sites (except the lake shore) are all small to moderate sized

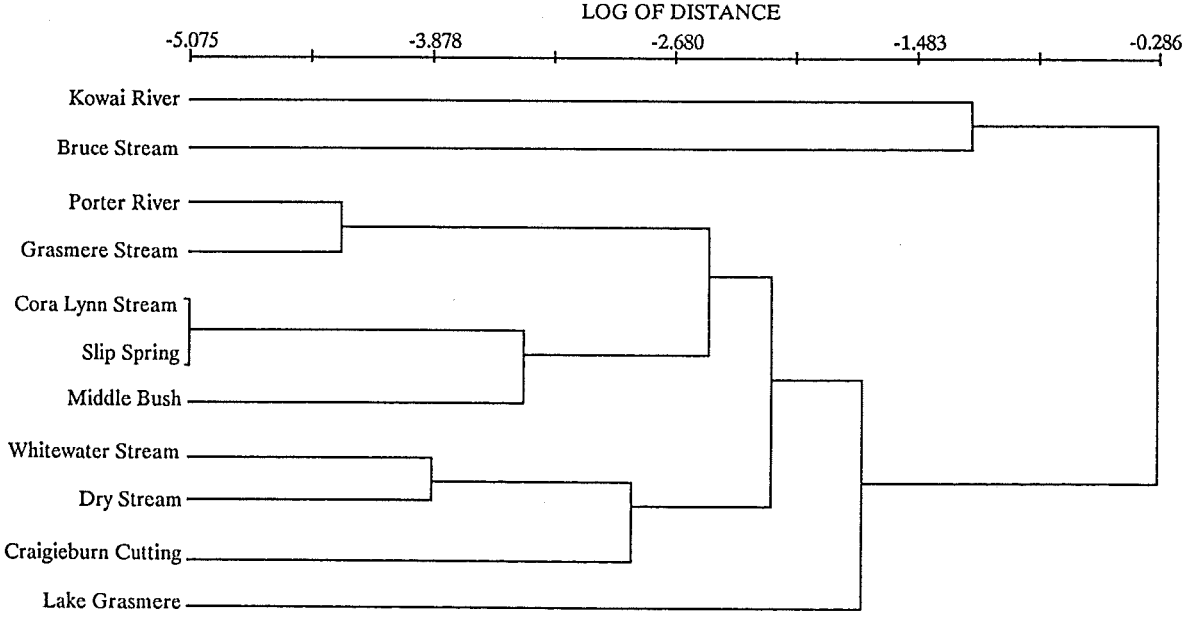


Figure 2.7. Cluster analysis of mean stability measurements (N.B. Pfankuch bottom values only and excluding the tractive force measure) for each of the study sites. Data were standardised with a norm transformation and temperature range measures downweighted by 0.5. The dendrogram was constructed using Euclidean distance and a group average clustering algorithm.

streams with similar physicochemical characteristics. All sites had moderately hard water, a circumneutral pH and low nutrient concentrations. Physically, they ranged in size from first to third order streams with a mean depth between 5 and 34 cm, mean width between 0.9 and 6.3 m, mean temperature between 8°C and 13°C and a mean current speed between 36 and 102 cm s^{-1}. Although these characteristics encompass a relatively wide range, both site groups (i.e., "stable" and "unstable") had representatives of small and moderate sized streams and there was little overall difference in the range of physicochemical conditions between the stable and unstable groups.

Most of the stability measurements indicated similar trends, although none of the measures assigned the same rank stability to each of the sites. The predicted substrate movement and total Pfankuch stability scores were the only two exceptions and did not conform well with any of the other stability measures. This was probably in part because of fundamental differences in the hydrologic nature of these streams (in contrast to the Northern Hemisphere streams for which both the Pfankuch and critical tractive force measures were developed), and also in part because they addressed hydrological stability rather than variation in the actual environment as measured by the other indices.

However, even if only the stability measures that exhibited similar trends are considered, there are still marked differences in the stability rankings assigned to each site. Thus, the use of only a single measure could give a misleading impression of "overall" stability, if such a condition exists, whereas to use each of the stability measures separately might be equally confusing. I have attempted to circumvent this problem by merging the separate stability measures in a combined index (i.e., the PCA scores).

Overall, environmental variability (as assessed by these stability measures) was considerably greater in the "unstable" sites than in the "stable" sites. However, while my initial classification, based on the nature of their source, divided the sites into two distinct groups, the stability measures yielded a ranking of the sites along a continuum from very stable to very unstable.

CHAPTER 3

EPILITHIC PERIPHYTON COMMUNITIES AND THE RETENTION OF ORGANIC MATERIAL

INTRODUCTION

The energetic base of a stream food web can range from one where energy is produced primarily within the stream itself (autochthonous based) to one where most of the energy inputs are from outside (allochthonous based) (Minshall, 1978; Bott, 1983). The relative contribution of the two energy sources within a stream may also change seasonally and as a result of disturbance (Cushing & Wolf, 1982).

Epilithic periphyton communities may comprise bacteria, cyanobacteria, eukaryotic algae, protozoa, fungi, amorphous detritus or any combination of these (Biggs & Close, 1989). The structure and biomass of the community is dependent on a number of hydrological, chemical and biological factors (Bott, 1983; Biggs, 1987).

Hydrological determinants appear to be of primary importance in many streams. Flood frequency and intensity (Tett *et al.*, 1978; Scrimgeour & Winterbourn, 1989), water velocity (McIntire, 1968; Lindstrom & Traaen, 1984) and substrate stability (Tett *et al.*, 1978; Robinson & Minshall, 1986) have all been shown to affect periphyton communities, although other limiting factors (e.g., light) may lessen such effects (Robinson & Minshall, 1986). Periphyton community composition is also affected by flood frequency and intensity, as some taxa (e.g., certain diatom species) are both more resistant to disturbances and better able to recolonise following disturbance than other taxa (e.g., filamentous green algae and cyanobacteria) (Fisher *et al.*, 1982; Grimm & Fisher, 1989).

Light is an obvious factor limiting periphyton growth, particularly in closed canopy streams (Rounick & Gregory, 1981; Triska *et al.*, 1983), and it also affects community composition of stone surface biofilms (Rounick & Winterbourn, 1983b). Concentrations of phosphorus (Peterson *et al.*, 1985) and nitrogen (Grimm & Fisher, 1986) in the water column have also been shown to affect epilithic algal growth in North American streams and rivers, and Winterbourn & Fegley (1989) and Winterbourn (1990) found that some of the forested and grassland streams included in my study are both nitrogen and phosphorus limited. Nutrients may in fact be more important growth limiting factors than light in some closed canopy streams (Winterbourn & Fegley, 1989). Biggs & Close (1989) and Biggs (1988) in their studies of a number of Canterbury rivers, found that both nutrient concentrations and hydrological determinants were important predictors of periphyton standing crops.

Invertebrate grazing may also affect periphyton biomass and composition (Lamberti & Resh, 1983; Hill & Knight, 1988) and studies by Ryder (1989), Winterbourn & Fegley (1989) and Winterbourn (1990) have demonstrated the poten-

tial for grazing impacts in a number of New Zealand streams, including a number of my study sites.

Although a number of studies have been conducted to investigate how afforestation and debris dam formation affects organic matter retention (e.g., Trotter, 1990; Webster *et al.*, 1990 and references therein) there appears to have been little corresponding work on the effects of stream bed stability and flooding on organic matter retention in open streams. Exceptions to this in New Zealand are the studies by Scrimgeour & Winterbourn (1989) and Graesser (1988) who both found particulate organic material collected in Surber samples was not related in any clear way to flood events. Similarly Webster *et al.* (1987) found that seston transport (particulate organic material entrained in the water column) was more closely related to substrate characteristics than discharge, although the rate of increase in discharge was an important determinant of seston concentration.

Although the principal aim of this section of work was to establish the energetic base of each of my stream food webs, it was also possible to examine the relationship between the epilithic communities, retention of organic material and physicochemical conditions at my study sites. To achieve this I measured organic layer development, epilithic periphyton biomass and particulate organic matter (in both the substrate and associated with stones used to sample the invertebrate fauna) at three monthly intervals between October 1987 and October 1988. I also examined the composition of the epilithic layers present on each of these sampling dates using scanning electron microscopy. I was then able to examine how these variables related to each of the stability measures and other hydrological and chemical parameters at the study sites over this period.

MATERIALS AND METHODS

Sampling Protocol

Collections were made on 23-24 October 1987 (spring 1), 23-25 January 1988 (summer), 23-25 April 1988 (autumn), 23, 30-31 July 1988 (winter) and 22-23 October 1988 (spring 2).

Periphyton

Periphyton biomass is difficult to measure directly because of its association with other stone surface organic components, such as fungi and bacteria (Wetzel & Westlake, 1974). Therefore, to estimate algal standing crops, photosynthetic pig-

ments (usually chlorophyll *a* and phaeophytin *a*) are generally measured (McConnell & Sigler, 1959; Moss, 1967a) as was done in this study.

Five cobbles (mean diameter = 6 cm) were collected at each site for pigment analysis, and were kept cool and dark during transport to the laboratory. Pigments were extracted with 90% acetone for 24 h in the dark at 5°C. Extract absorbances were read at 410, 430, 665 and 720 nm against a solvent blank on a Kontron Uvikon 860 Spectrophotometer, and chlorophyll *a* and phaeophytin *a* concentrations were calculated using the method of Moss (1967a, b). For this, a single standard curve, based on a series of curves for a number of algal community types (given in Moss, 1967a) was used. Both pigments were combined to give an estimate of total algal accumulation, irrespective of physiological state, as this is considered to provide a better estimate of algal biomass than chlorophyll *a* alone (Hawkins *et al.*, 1982). Total pigment concentration was highly correlated with both chlorophyll *a* ($r_s = 0.99, df = 273, P < 0.05$) and phaeophytin *a* ($r_s = 0.68, df = 273, P < 0.05$) concentrations. Stone surface area was measured by wrapping the stones upper surface in aluminium foil of known weight per unit area, and pigment concentrations were expressed per unit stone surface area.

Periphyton community structure was examined using scanning electron microscopy (SEM). Clean stone chips, glued to aluminium SEM stubs, were incubated in the stream in perspex holders attached to large boulders. After three months, stubs were collected and preserved in 3% gluteraldehyde in phosphate buffer. This procedure was carried out on each of the above sampling dates. When boulders were lost from some of the more unstable streams, stone chips of similar size (mean diameter = 1.5 cm) were collected from the stream substrate. All stone chips were washed twice in phosphate buffer, dehydrated in an alcohol series (Rounick & Winterbourn, 1983b) and dried in a vacuum desiccator. Following coating with 50 nm of carbon/gold they were examined with a Cambridge Stereoscan MK II scanning electron microscope at 15,000 - 20,000 khtz. Algae were identified to the lowest possible taxonomic level (usually genus) using Weber (1971), Foged (1979) and Pridmore & Hewitt (1982).

Epilithic carbon

Stone surface organic carbon was measured on five stones from each site (mean diameter = 3 cm) collected and frozen on each sampling occasion. Organic carbon was measured with the micro-dichromate oxidation technique (Maciolek, 1962; Newell, 1982) using heat-by-dilution, as modified by Collier (1987). Concentrations were expressed per unit stone surface area (measured using aluminium foil).

Particulate organic carbon

Five 220 ml core samples (4.5 cm diameter) of substrate were collected at each site, frozen and returned to the laboratory. Samples were separated into two components; coarse (> 1 mm) and fine (> 5 μm and < 1 mm). They were dried to constant weight at 66°C for a minimum of 7 days and ashed at 550°C for 6 h, the difference in weight before and after ashing being a measure of the particulate organic carbon in the sample.

Particulate organic material (including any attached bryophytes) associated with invertebrate stone samples (refer Chapter 4) was also measured. Samples were preserved in 10% formalin and returned to the laboratory. After removal of the invertebrates, organic matter was elutriated off, dried to constant weight at 66°C for a minimum of 7 days, and weighed. The amount of organic matter present in a 0.1 m^2 area of stream bed was calculated as described by Wrona *et al.* (1986) (refer Chapter 4).

Analysis

Data were analysed with the regression, stepwise regression and Spearman rank correlation procedures of SAS (1985). Stepwise regression of total pigment and epilithic carbon concentration was carried out using the 20 chemical, physical and stability measurements listed in Table 3.1. Concentrations of both total pigment and epilithic carbon were log (x+1) transformed prior to this analysis. Spot measurements are those made at the time of collection or in the month prior to the collection of samples. The critical probability for addition and removal of variables to the model was set at 0.05. The same variables were used in the correlation analysis.

RESULTS

Periphyton

Pigment concentrations

Mean total pigment concentrations, for the five stones collected at each site are plotted in Fig. 3.1. Mean maximum biomass at the sites ranged from 15.4 μg cm^{-2} at Slip Spring to 0.7 μg cm^{-2} at Bruce Stream; mean minimum biomass ranged from 4.6 μg cm^{-2} at Lake Grasmere to 0 μg cm^{-2} at several sites. In general, the more stable sites had maximum biomass in winter and autumn, whereas the unstable sites had maxima in one of either of the two spring samples.

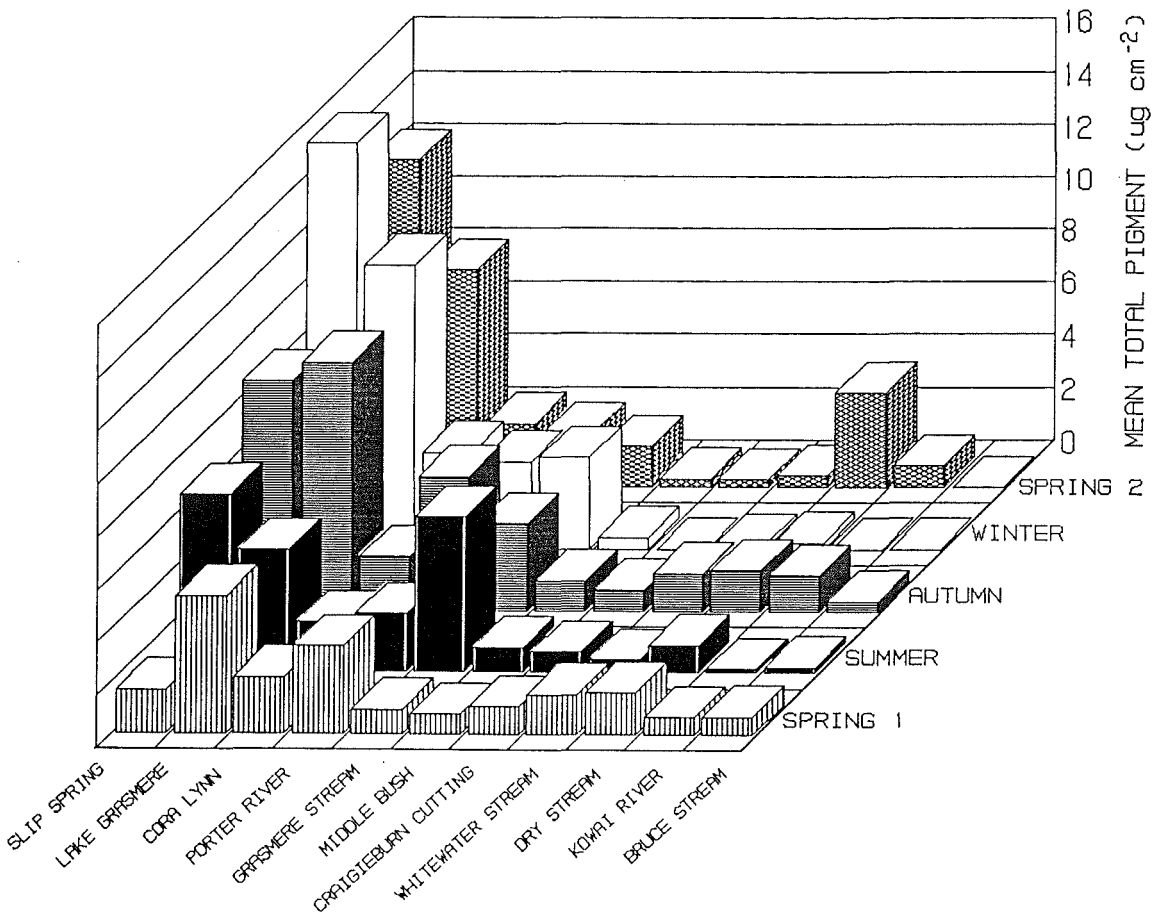


Figure 3.1. Mean pigment concentrations (n = 5) on cobbles collected from the study sites between October 1987 and October 1988.

Mean algal biomass (total pigment concentration) decreased logarithmically as overall environmental stability (multivariate stability scores) decreased (F = 158.24, df = 1,269, $P < 0.05$, r^2 = 0.38) (Fig. 3.2). Mean biomass at the two forest streams fell well below this line, perhaps indicating that light limitation rather than stability was more important to algal communities at these sites. Removal of these two sites from the analysis improved the fit of the model (r^2 = 0.50).

A similar trend of decreasing algal biomass with decreasing stability was evident in each of the seasons, however, the specific nature of the relationship was different (i.e., there was a significant interaction between the effect of stability and the season) (F = 3.84, df = 4,265, $P < 0.05$). This reflects the fact that stable and unstable sites have maximum and minimum algal biomass in different seasons. All lines had a slope significantly different from zero, with winter exhibiting the biggest difference between stable and unstable sites (i.e., the steepest relationship with a slope = -0.50) and spring 1 the least (i.e., the flattest slope = -0.17). As the slopes of the seasonal relationships were different, it is not valid to compare seasonal effects (Sokal & Rohlf, 1981). Nevertheless, overall, winter had the highest mean (3.4 μg cm^{-2}) and spring 1, the lowest (1.8 μg cm^{-2}).

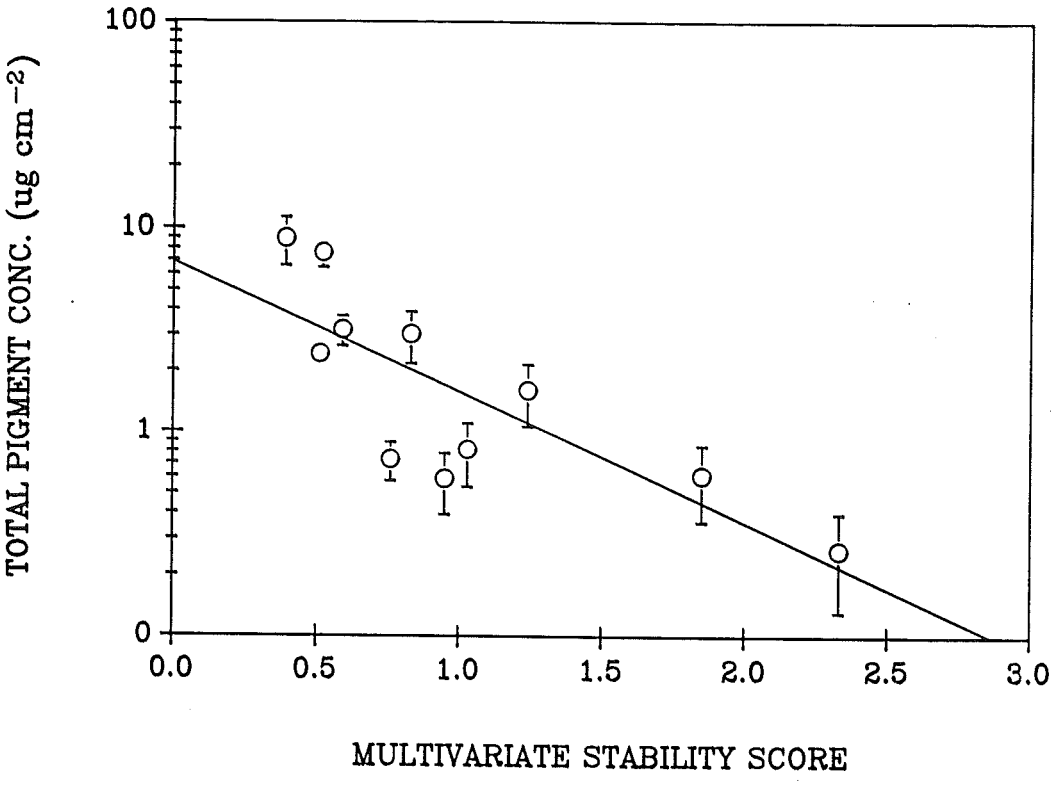


Figure 3.2. Mean periphyton biomass (pigment concentration) at each study site as a function of overall stability (multivariate stability score). Plotted values are averages of the seasonal means ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, $\log_{10}$ (pigment conc.) = 0.76 - 0.34(stability score), r^2 = 0.38.

Spatial variation in pigment concentrations (coefficient of variation of values for the five replicate stones collected at each site) (Fig. 3.3) was not related to environmental stability (F = 2.79, df = 1,49, P > 0.05). However, as the stability of a site decreased, seasonal variation (coefficient of variation of mean algal biomass across the seasons) (Fig. 3.3) increased (F = 76.86, df = 1,9, P < 0.05, r^2 = 0.90). Slip Spring (the most stable site) was the only site to deviate radically from this trend. Just prior to beginning this study it was subjected to cattle grazing nearby weed beds, a disturbance that reduced periphyton levels; removal of this value halved its coefficient of variation and brought it more into line with the model. The ratio of phaeophytin *a* to chlorophyll *a* (a measure of the proportion of dead to live algae) was also unrelated to environmental stability (F = 0.06, df = 1,49, P > 0.05) as the highest ratios occurred in the streams of intermediate stability (e.g., Dry Stream and Whitewater Stream).

Correlations of algal biomass with a number of other physicochemical variables are given in Table 3.1. The only chemical variable correlated significantly with algal biomass was mean alkalinity and the only physical variable correlated was mean current velocity. All stability characteristics were significantly and negatively correlated with periphyton biomass.

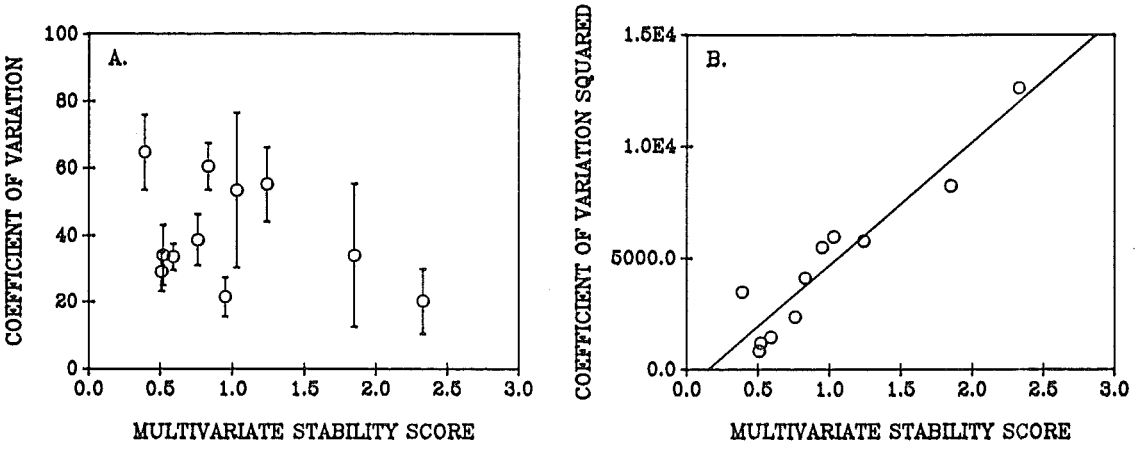


Figure 3.3. A. Mean (± 1 SE) of the coefficient of variation of pigment concentration on five replicate stone samples (spatial variation) collected in each season at the study sites plotted against overall stability (multivariate stability score). The relationship was not significant, $r^2 = 0.08$.

B. Coefficient of variation of pigment concentration at the eleven study sites, based on mean values obtained in five seasons, plotted against overall stability. Regression analysis yielded the equation, (Seasonal CV)^2 = 5518.5(stability score) - 843.67, $r^2 = 0.90$.

The single best predictor of algal biomass (Table 3.2) in each of the seasons and overall (i.e., all the means pooled together) was the bottom component of the Pfankuch index (r^2 = 0.45-0.67). As stability decreased (i.e., at higher Pfankuch index scores), algal biomass decreased. The other important predictor of mean biomass over all the seasons was mean temperature which was positively associated with periphyton biomass. It is interesting to note that spot temperature measurements (which reflect seasonal changes) were not more important than overall average stream temperature, but this probably reflects the biomass peaks of stable and unstable streams in different seasons. Other variables that were important for predicting algal biomass according to the multivariate models differed with season, and because of the additive nature of the model, did not always reflect the same functional response that they would have alone. All models fitted the data well and a large proportion of the variation in the data was explained by the models in all seasons (r^2 = 0.72-0.88) and overall (r^2 = 0.62).

Removal of the two forested sites from the stepwise regression analysis (this was done because they may have behaved differently from the other sites because of their lower light levels) yielded important variables that were dependent on the season (Table 3.3). Current variability, the Pfankuch bottom component, overall stability, spot temperature range, and mean current velocity were the single most important variables in spring 1, summer, autumn, winter and spring 2, respectively. Improvements in the ability of the model to explain the data with these two sites removed were not great however, ranging from an increase of 9% to a decrease of 6%. For all the seasons pooled the Pfankuch bottom component was the only important variable (r^2 = 0.56).

Table 3.1. Correlation (r_s) of total pigment concentration and total organic carbon with a number of hydrological and chemical parameters. The hydrological and chemical parameters were measured monthly at the study sites between October 1987 and May 1989 (see Chapter 2). * indicates significant correlations at P = 0.05.

Physicochemical parameter	Total pigment	Total organic carbon
CHEMICAL		
Spot conductivity	0.09	0.24
Spot pH	0.01	0.20
Mean conductivity	0.03	0.21
Mean pH	0.03	0.10
Mean alkalinity	0.35*	0.40*
PHYSICAL		
Spot current velocity	-0.25	-0.28*
Spot depth	0.003	-0.06
Spot temperature	0.26	0.40*
Mean current velocity	-0.32*	-0.34*
Mean depth	-0.04	-0.05
Mean temperature	0.06	0.05
STABILITY		
Spot temperature range	-0.39*	-0.38*
Mean temperature range	-0.49*	-0.46*
Current variation	-0.40*	-0.44*
Depth variation	-0.27*	-0.28*
Spot stone movement	-0.62*	-0.71*
Mean stone movement	-0.78*	-0.68*
Pfankuch bottom component	-0.80*	-0.76*

Community composition

No clear seasonal trends were observed in periphyton community composition, although the less stable sites showed a decrease in abundance of algae in the winter and spring 2 samples, when increased flows were more common. Algae taxa recorded on the stone surfaces at each of the study sites are listed in Table 3.4, with representative SEM micrographs for each of the unstable and stable sites in Plates 3.1 and 3.2, respectively.

Epilithic carbon

All but one unstable site (Whitewater Stream) had peak epilithic carbon concentrations in autumn, whereas the stable sites generally showed peaks in either the

Table 3.2. Results of the stepwise regression analysis of mean total pigment concentration against 20 physicochemical and stability measurements. Pigment concentrations were log (x+1) transformed before the analysis. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Variable removed	Parameter estimate	Partial r^2	Model r^2
SPRING 1				
Intercept		-1.52		
Pfankuch bottom component		-0.02	0.47	0.47
Mean pH		0.38	0.10	0.56
Mean conductivity		-0.002	0.09	0.65
Depth variation		0.01	0.05	0.70
Spot conductivity		-0.001	0.02	0.72
SUMMER				
Intercept		1.29		
Pfankuch bottom component		-	0.57	0.57
Tractive force		-0.01	0.04	0.61
Mean temperature range		-0.07	0.14	0.75
	Pfankuch bottom component	-		0.75
AUTUMN				
Intercept		-0.59		
Pfankuch bottom component		-0.01	0.59	0.59
Mean temperature		-	0.08	0.67
Spot conductivity		-	0.05	0.72
Spot temperature range		-0.06	0.02	0.75
Spot pH		0.29	0.02	0.77
	Mean temperature	-	-	0.76
Tractive force		-0.004	0.05	0.81
Mean conductivity		-0.01	0.02	0.83
	Spot conductivity	-	-	0.82
Mean alkalinity		0.02	0.01	0.84
WINTER				
Intercept		2.18		
Pfankuch bottom component		-0.05	0.67	0.67
Spot depth		0.01	0.05	0.72
SPRING 2				
Intercept		7.83		
Pfankuch bottom component		-0.06	0.45	0.45
Spot pH		-0.54	0.16	0.61
Spot current velocity		-1.79	0.13	0.74
Current variation		0.02	0.04	0.78
Mean temperature		-0.10	0.08	0.86
Overall stability		0.24	0.02	0.88
ALL SEASONS COMBINED				
Intercept		1.46		
Pfankuch bottom component		-0.03	0.59	0.59
Mean temperature		0.03	0.03	0.62

Table 3.3. Results of the stepwise regression analysis of mean total pigment concentration, excluding the two forested sites, against 20 physicochemical and stability measurements. Pigment concentrations were log (x+1) transformed before the analysis. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Variable removed	Parameter estimate	Partial r^2	Model r^2
SPRING 1				
Intercept		-2.23		
Current variation		-	0.54	0.54
Mean pH		0.44	0.04	0.59
Pfankuch bottom component		-0.02	0.07	0.66
	Current variation	-	-	0.66
Spot conductivity		-0.001	0.09	0.75
SUMMER				
Intercept		1.28		
Pfankuch bottom component		-	0.55	0.55
Tractive force		-0.01	0.05	0.59
Mean temperature range		-0.07	0.17	0.76
	Pfankuch bottom component	-		0.75
AUTUMN				
Intercept		1.23		
Overall stability		-0.36	0.56	0.56
Mean depth		0.02	0.09	0.65
Mean conductivity		-0.004	0.07	0.71
Mean current velocity		-0.004	0.05	0.76
Spot temperature range		-0.03	0.06	0.82
WINTER				
Intercept		1.23		
Spot temperature range		-0.17	0.73	0.73
Tractive force		-0.004	0.07	0.81
SPRING 2				
Intercept		2.03		
Mean current velocity		-	0.48	0.48
Spot temperature range		-0.10	0.18	0.65
Spot current velocity		-1.57	0.12	0.78
Spot conductivity		-0.002	0.05	0.82
	Mean current velocity	-	-	0.82
Depth variation		0.02	0.03	0.85
ALL SEASONS COMBINED				
Intercept		1.70		
Pfankuch bottom component		-0.03	0.56	0.56

Table 3.4. Composition of periphyton communities on stones collected from the study sites between October 1987 and October 1988.

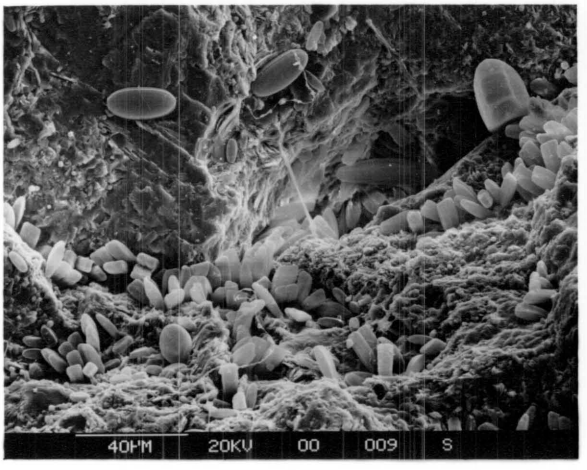
SITES	Dominant taxa	Common taxa	Rare taxa	Comments
UNSTABLE				
Kowai River	*Achnanthes lanceolata*	*Gomphonema* *Cocconeis*	filamentous green algae[1] coccoid blue green algae[1]	Stone surfaces at this site were mostly bare and diatoms, when present occurred mainly within crevices.
Whitewater Stream	filamentous blue green algae (probably *Lyngbya*) coccoid blue green algae	filamentous green algae[2] *Diatoma*[2]	*Gomphonema* *A. lanceolata*	The epilithon was composed primarily of an amorphous organic matrix with patches of algae within the matrix.
Dry Stream	coccoid blue green algae *Gomphonema* (at least two species) *Gomphoneis* *Cocconeis*	*Synedra* filamentous green algae filamentous blue green algae (probably *Lyngbya*) filamentous diatoms (mainly *Diatoma*)	*A. lanceolata* *Cymbella*	This site had a moderate density of both blue green algae and several species of diatom. Of the unstable sites this showed the greatest variability in species composition amongst seasons.
Craigieburn Cutting Stream	*Cocconeis* *A. lanceolata*		*Gomphonema* filamentous blue greens (probably *Lyngbya*) coccoid blue green algae	Diatoms present at this site were sparsely and patchily distributed over stone surfaces.
Bruce Stream			*Gomphonema* *A. lanceolata* coccoid blue green algae	Very few algae were observed at this site . Stone surfaces were mainly bare rock and algae, when recorded, were always in crevices.
STABLE				
Porter River	coccoid blue green algae filamentous blue green algae (probably *Lyngbya*)	*A. lanceolata* *Gomphonema* *Cocconeis* filamentous green algae *Gomphoneis*[3] *Synedra*[3] *Cymbella* (at least two species)[3]	*Fragilaria* *Achnanthes minutissima* *Triceratium alternans*	Diversity was greatest in the summer and autumn samples.

Slip Spring	coccoid blue green algae	*Diatoma* *Cymbella* *A. lanceolata* *A. minutissima*	*Gomphonema* *Navicula* *Cocconeis*	Stones had a dense uniform covering of a number of diatom species and the coccoid blue green algae.
Cora Lynn Stream	*Gomphonema* *A. lanceolata* *A. minutissima* *Cymbella* coccoid blue green algae	filamentous green algae *Diatoma*	*Cocconeis* [4]	This site always had a dense and uniform cover made up of a variety of species.
Middle Bush Stream	*Cocconeis* *A. lanceolata*		*Rhoicosphenia* *Gomphonema* coccoid blue green algae	Except in the summer sample, when densities were higher, diatoms were sparsely and patchily distributed over stone surfaces.
Grasmere Stream	coccoid blue green algae in an organic matrix filamentous blue green algae (probably *Lyngbya*) *Cymbella* *A. minutissima* *Gomphonema*		Filamentous green algae *Cocconeis* *Synedra* *Fragilaria*	Of the stable sites, this exhibited the most seasonal changes.
Lake Grasmere	*Synedra* *Gomphoneis*	*Cocconeis* *A. minutissima* *A. lanceolata* coccoid blue green algae	*Diatoma* *Cymbella* *Cyclotella*	Periphyton communities at this site were heavily dominated by *Synedra*.

1 Spring 1 only.
2 The two spring and autumn samples only.
3 In summer and autumn.
4 Only in summer and winter.

Plate 3.1. Scanning electron micrographs of periphyton communities on stones from the unstable sites: A) Kowai River (spring 1), B) Dry Stream (summer), C) Whitewater Stream (summer), D) Craigieburn Cutting Stream (summer) and E) Bruce Stream (autumn).

A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B


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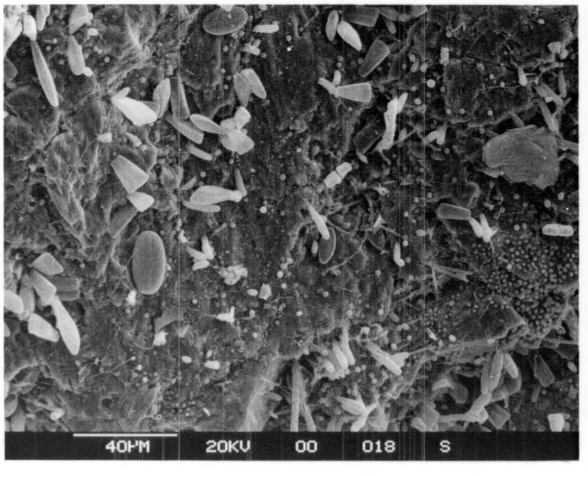
C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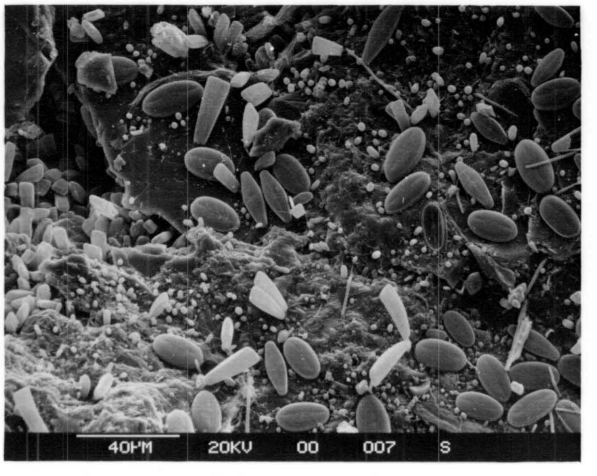
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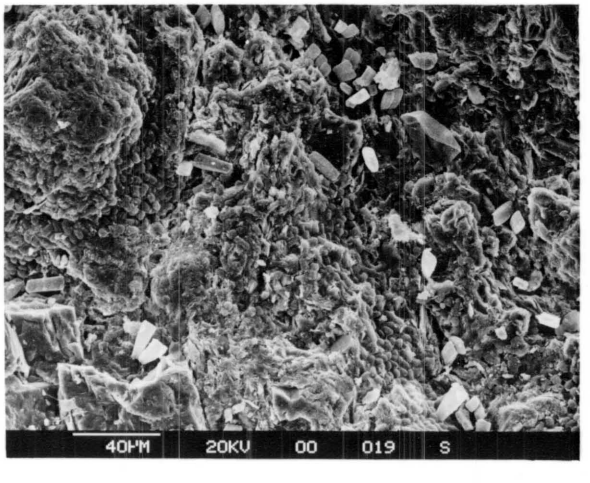
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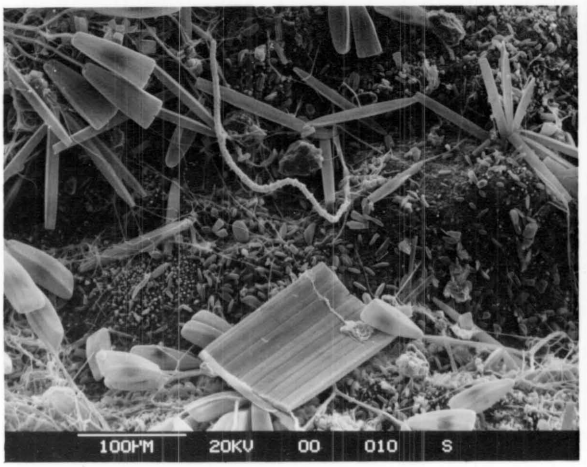
Plate 3.2. Scanning electron micrographs of periphyton communities on stones from the stable sites: A) Slip Spring (summer), B) Porter River (summer), C) Middle Bush Stream (summer), D) Grasmere Stream (summer), E) Cora Lynn Stream (spring 2) and F) Lake Grasmere (spring 1).

A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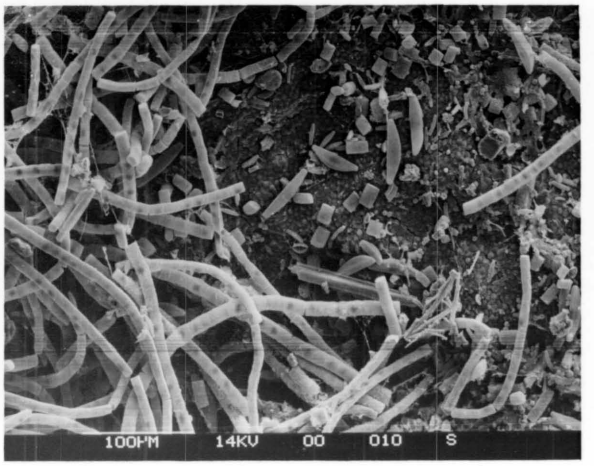
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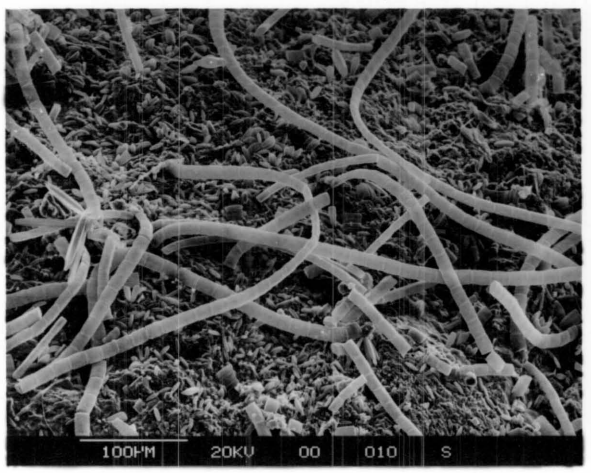
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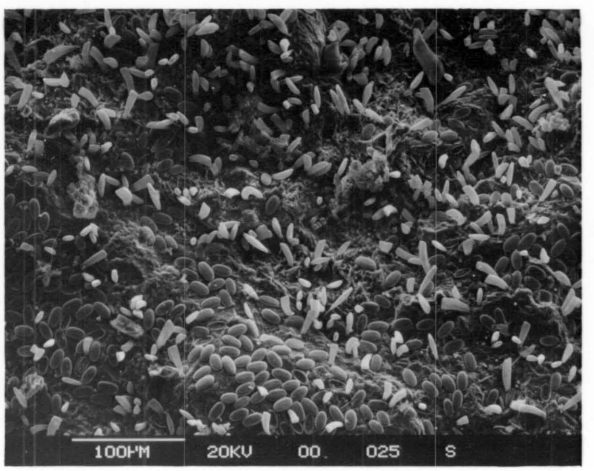
D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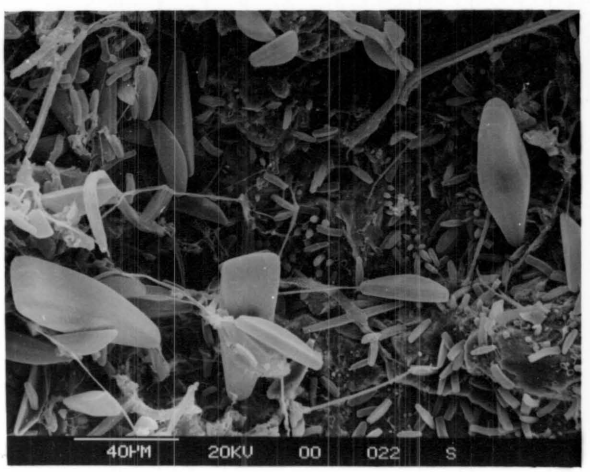
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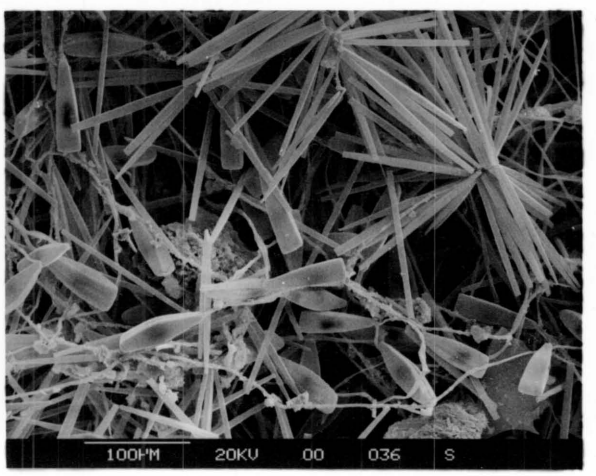
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first spring or summer samples (Fig. 3.4). Peak carbon concentrations ranged from 37.8 μg cm^{-2} in Lake Grasmere to 2.6 μg cm^{-2} at Bruce Stream. Mean epilithic carbon concentrations were significantly correlated with pigment concentrations (algal biomass) (r_s = 0.70, df = 273, P < 0.05), but seasonal peaks did not correspond with peaks in algal biomass. However, the ratio of algal pigment concentration to epilithic carbon concentration was not related to the overall stability (i.e., multivariate stability scores) of a site (F = 2.19, df = 1,49, P > 0.05).

Mean epilithic carbon concentrations decreased logarithmically with a decrease in overall environmental stability (F = 183.14, df = 1,269, P < 0.05, r^2 = 0.48) (Fig. 3.5). The same general relationship existed in each season, however, the nature of the relationship was significantly different between seasons (F = 5.93, df = 4,265, P > 0.05). This again reflected different seasonal responses by stable and unstable sites and did not allow a comparison of seasonal means. However, spring 2 had the lowest overall mean epilithic carbon concentrations (6.0 μg cm^{-2}) and autumn the highest concentrations (16.0 μg cm^{-2}). The difference in carbon concentrations between stable and unstable sites was greatest in summer (this season had the steepest relationship, with the slope = -0.76) and least in spring 2

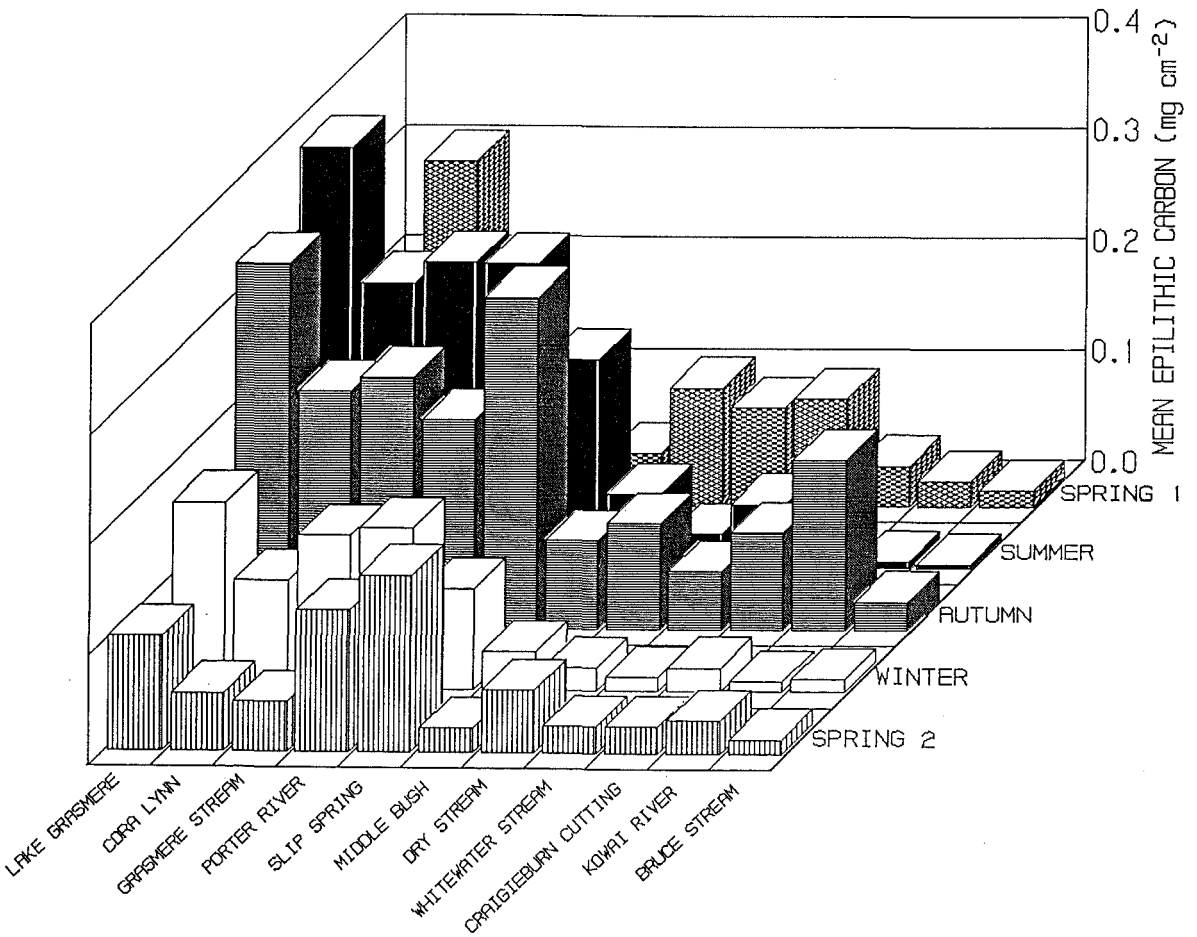


Figure 3.4. Mean epilithic carbon concentration (n = 5) on cobbles collected from the study sites between October 1987 and October 1988.

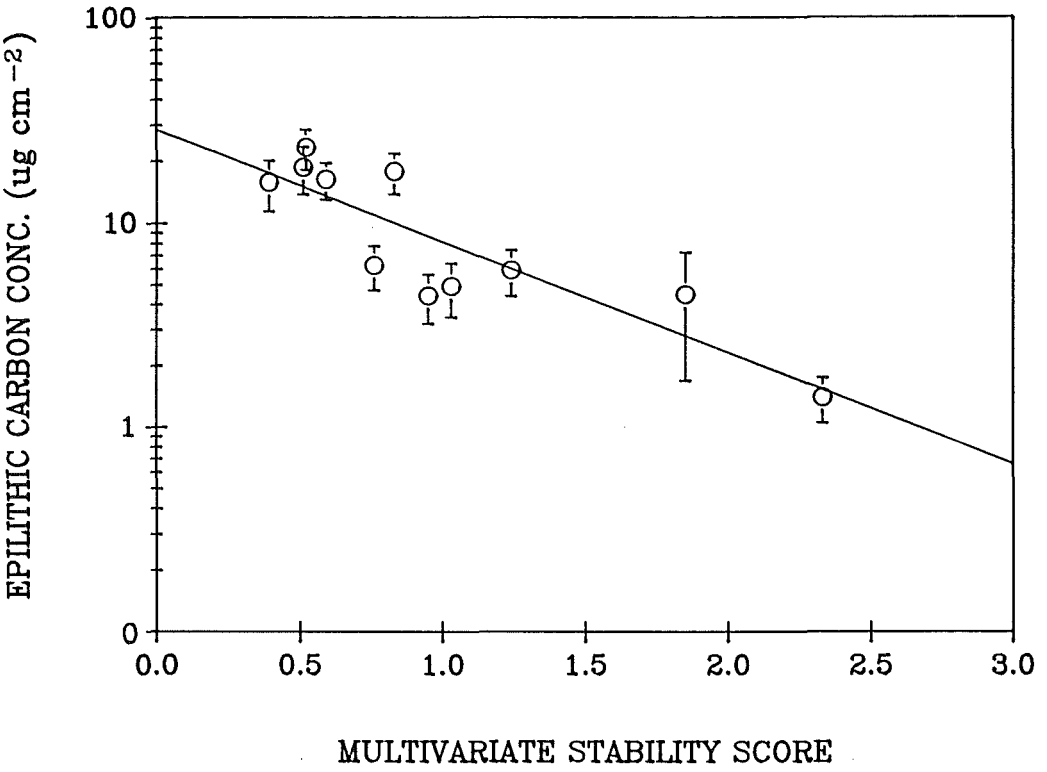


Figure 3.5. Mean epilithic carbon concentration plotted against overall stability. Values are averages of seasonal means ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, $\log_{10}$ (carbon conc.) = 1.18 - 0.46(stability score), r^2 = 0.46.

(this had the shallowest relationship, with the slope = -0.33).

Spatial variation in epilithic carbon concentrations (coefficient of variation of values for the five replicate stones collected at each site) showed a significant increase with a decrease in overall stability (F = 5.05, df = 1,49, P < 0.05) (Fig. 3.6).

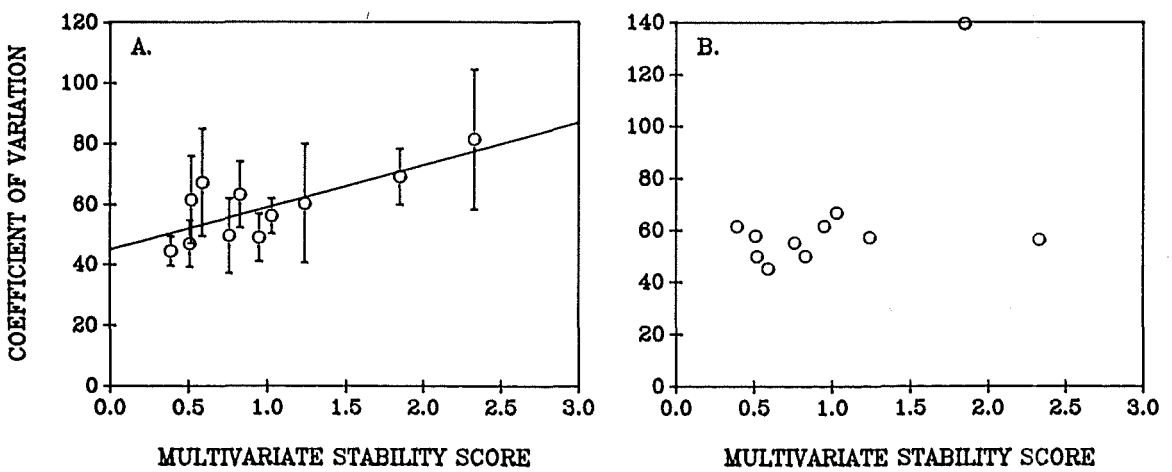


Figure 3.6. A. Mean (± 1 SE) of the coefficient of variation of epilithic carbon concentration on five replicate stone samples (spatial variation) collected in each season at the study sites plotted against overall stability. Regression analysis yielded the equation, Spatial CV = 43.45 + 13.98(stability score), r^2 = 0.25.

B. Coefficient of variation of epilithic carbon concentration at the eleven study sites, based on mean values obtained in five seasons, plotted against overall stability. The relationship was not significant, r^2 = 0.24.

However, only the summer sample had a slope significantly greater than zero, and when it was removed from the analysis the relationship was non significant (F = 0.70, df = 1,39, P > 0.05). Seasonal variation in carbon concentrations (coefficient of variation of mean epilithic carbon concentrations across the seasons) was not related to overall environmental stability (F = 2.77, df = 1,9, P > 0.05) (Fig. 3.6).

The relationship between epilithic carbon concentration and other physicochemical factors is given in Table 3.1. Concentrations were positively correlated with mean alkalinity and spot temperature measurements, and negatively correlated with mean and spot current velocities. All stability values were negatively correlated with mean epilithic carbon concentration.

As for algal biomass, the best predictor of epilithic carbon concentrations in all but one season (spring 1, when mean stone movement score was the best predictor) was the bottom component of the Pfankuch index (r^2 = 0.42-0.75) (Table 3.5). Organic carbon concentrations decreased as the Pfankuch index increased (i.e., as stability decreased). Other variables that were important in multivariate models for predicting epilithic carbon concentrations differed between seasons, with regression equations explaining from 51 to 78% of the variation in the data. Pooled seasonal values were also predicted best by the Pfankuch bottom component, with spot stone movement and mean depth also important (total r^2 = 0.69).

Particulate Organic Material

The mean biomass of particulate organic material (POM) collected in core samples at each of the sites is plotted in Fig. 3.7. Peak POM concentrations ranged from 22.2 g l^{-1} at Middle Bush Stream to 10.7 g l^{-1} at Porter River. No clear seasonal trends were observed in either stable or unstable streams, however, and little variation was found between seasons (coefficient of variation between seasonal means ranged between 5.4% and 37.7%).

Furthermore no clear relationship was found between total particulate organic matter and the overall stability (i.e., the multivariate stability scores) of a site (F = 0.0, df = 1,234, P > 0.05) (Fig. 3.8). This situation also applied to both coarse (CPOM) and fine particulate organic material (FPOM) when analysed separately (F = 0.02, df = 1,199, P > 0.05 and F = 0.36, df = 1,237, P > 0.05 for CPOM and FPOM, respectively). The ratio of fine to coarse particulate organic material did, however, appear to be related to overall stability (F = 6.34, df = 1,203, P < 0.05), increasing as stability decreased; however, only the spring 2 sample had a slope significantly greater than zero (i.e., the significant increase only occurred in this season).

Table 3.5. Results of the stepwise regression analysis of mean epilithic carbon concentration against 20 physicochemical and stability measurements. Epilithic carbon concentrations were log (x+1) transformed before the analysis. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Variable removed	Parameter estimate	Partial r^2	Model r^2
SPRING 1				
Intercept		0.71		
Mean stone movement		-0.01	0.30	0.30
Mean conductivity		0.01	0.16	0.46
Tractive force		-0.004	0.05	0.51
SUMMER				
Intercept		3.41		
Pfankuch bottom component		-0.06	0.75	0.75
AUTUMN				
Intercept		1.32		
Pfankuch bottom component		-0.02	0.42	0.42
Mean temperature		0.10	0.11	0.53
Spot temperature range		-0.07	0.19	0.72
Spot current velocity		-0.39	0.06	0.78
WINTER				
Intercept		2.09		
Pfankuch bottom component		-0.04	0.56	0.56
Spot depth		0.01	0.05	0.61
Mean temperature range		-0.04	0.04	0.65
SPRING 2				
Intercept		1.76		
Pfankuch bottom component		-0.04	0.44	0.44
Mean conductivity		-0.004	0.09	0.53
Tractive force		0.01	0.04	0.57
Mean temperature		0.06	0.04	0.61
ALL SEASONS COMBINED				
Intercept		1.88		
Pfankuch bottom component		-0.03	0.58	0.58
Spot stone movement		-0.004	0.07	0.65
Mean depth		0.01	0.04	0.69

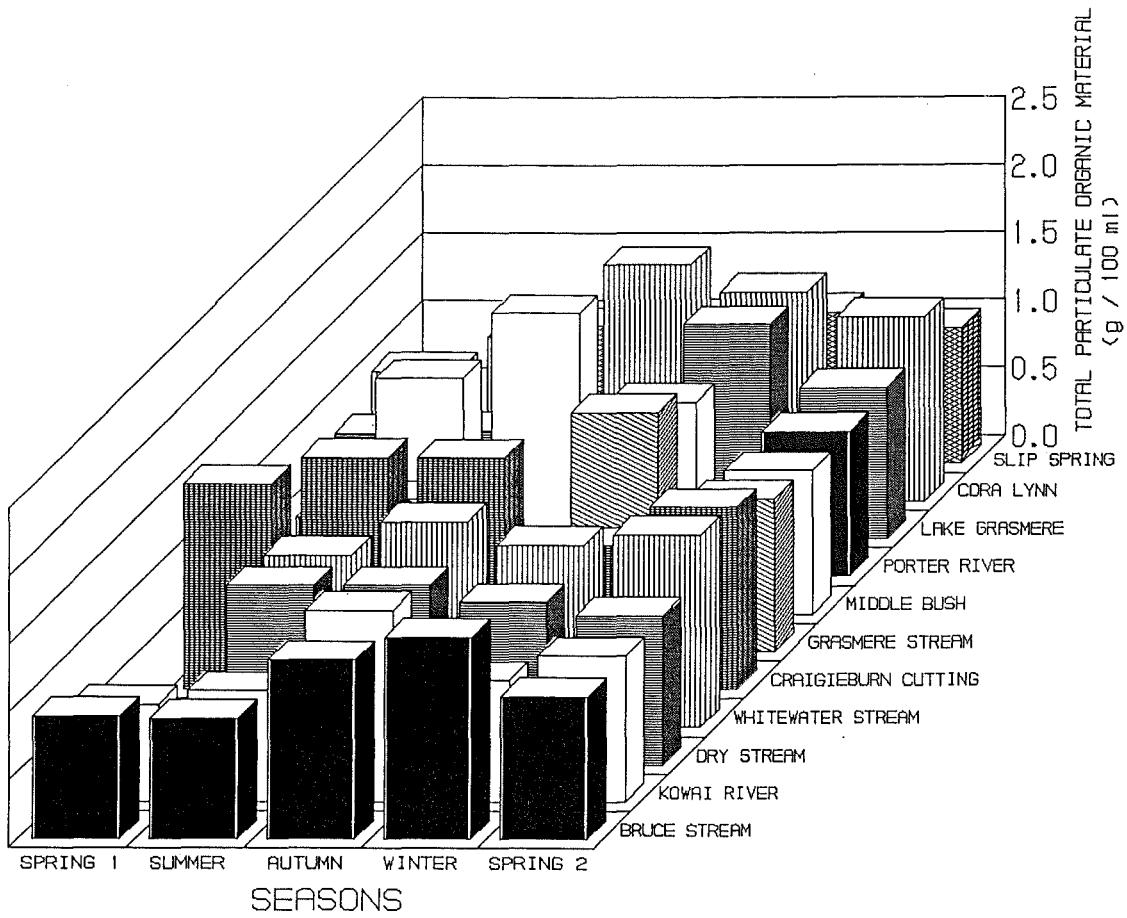


Figure 3.7. Mean biomass of total particulate organic material (POM) (n = 5) in core samples collected from the study sites between October 1987 and October 1988.

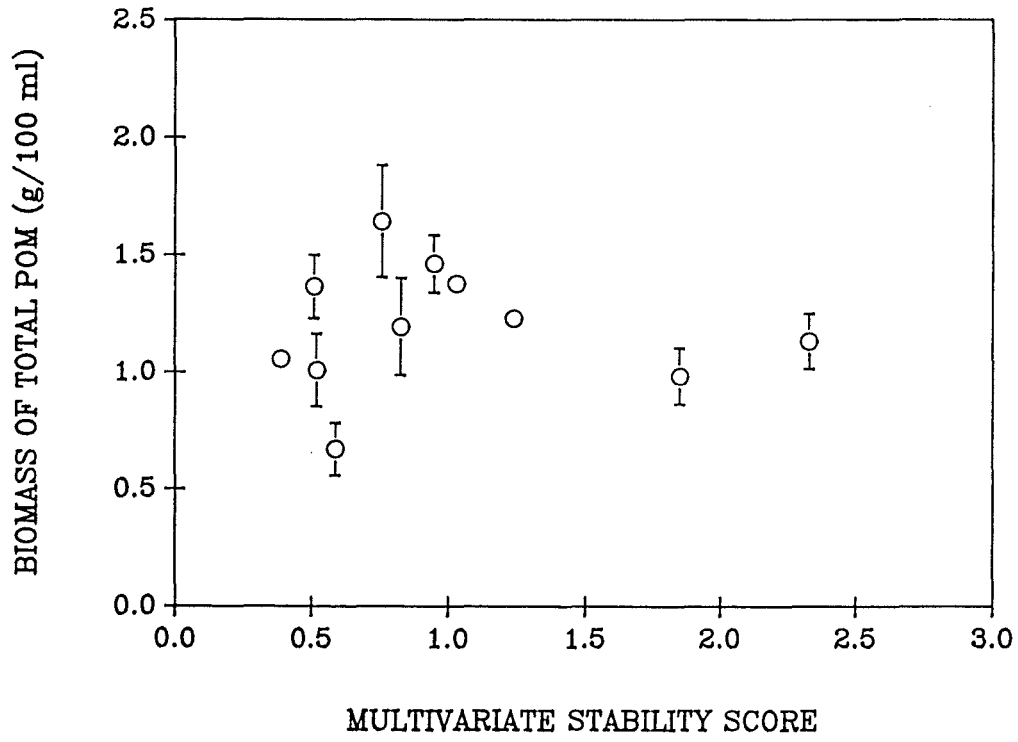


Figure 3.8. Mean biomass of total particulate organic material (POM) as a function of overall stability. Plotted values are averages of the seasonal means ± 1 SE. The relationship was not significant, $r^2 = 0.05$.

Neither spatial variation (coefficient of variation amongst the five replicate core samples from a site) (Fig. 3.9), nor seasonal variation (coefficient of variation amongst seasonal means) (Fig. 3.9) were related to the stability of a site (F = 0.02, df = 1,44, $P > 0.05$ and F = 0.02, df = 1,9, $P > 0.05$ for spatial and seasonal variation, respectively).

Correlation coefficients for total POM, CPOM and FPOM with a number of physicochemical variables are given in Table 3.6. Total and coarse particulate material were negatively correlated with spot depth and temperature measurements and the mean depth and current speed of a site, whereas FPOM was only correlated with the mean temperature of a site. Although significant, these relationships are still weak and probably reflect the fact that the two forested streams, which had higher organic input, were small. None of the stability measurements was correlated with any of the particulate carbon measurements.

In contrast to the POM in core samples, the amount of organic matter associated with stone samples was significantly higher at the more stable sites (F = 45.8, df = 1,49, $P < 0.05$, r^2 = 0.50) (Fig. 3.10). In fact, stable and unstable sites tended to group separately, with a sharp transition between the two. As for the core samples, however, no clear seasonal trends were apparent (Fig. 3.11), with maximum and minimum values 312 g m^{-2} (Middle Bush) and 10 g m^{-2} (Kowai River), respectively.

Spatial variation amongst organic matter associated with the stone samples was not related to overall stability (F = 0.12, df = 1,49, $P > 0.05$) (Fig. 3.12). However,

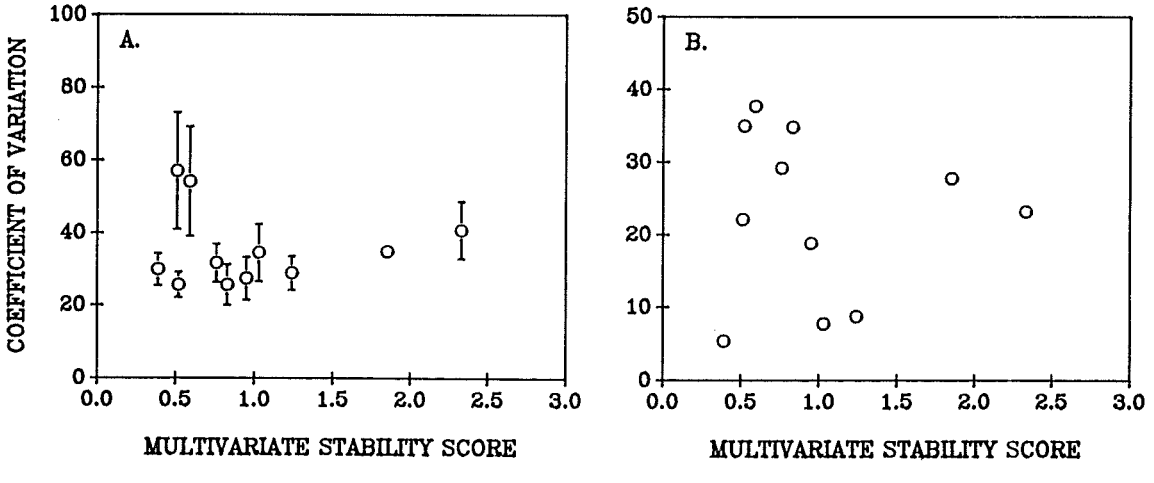


Figure 3.9. A. Mean (± 1 SE) of the coefficient of variation of total particulate organic material (POM) in five replicate core samples (spatial variation) collected in each season at the study sites plotted against overall stability. The relationship was not significant, r^2 = 0.09.

B. Coefficient of variation of total particulate organic material (POM) at the eleven study sites, based on mean values obtained in five seasons, plotted against overall stability. The relationship was not significant, r^2 = 0.003.

Table 3.6. Correlations (r_s) between total, fine, coarse and stone associated particulate organic carbon and a number of hydrological and chemical parameters. The hydrological and chemical parameters were measured monthly at the study sites between October 1987 and May 1989 (see Chapter 2). * indicates significant correlations at $P = 0.05$.

Physicochemical parameter	Total particulate carbon	Coarse particulate carbon	Fine particulate carbon	Stone associated POM
CHEMICAL				
Spot conductivity	0.01	-0.04	0.02	0.13
Spot pH	0.25	0.27	-0.01	0.08
Mean conductivity	0.11	-0.01	0.11	0.30*
Mean pH	-0.03	-0.05	-0.06	0.05
Mean alkalinity	0.05	-0.01	0.07	0.44*
PHYSICAL				
Spot current velocity	-0.21	-0.26	0.06	-0.23
Spot depth	-0.28*	-0.33*	-0.07	-0.32*
Spot temperature	-0.39*	-0.29*	-0.16	0.06
Mean current velocity	-0.34*	-0.30*	-0.14	-0.50*
Mean depth	-0.41*	-0.44*	-0.27	-0.47*
Mean temperature	-0.27	-0.18	-0.31*	-0.45*
STABILITY				
Spot temperature range	-0.06	-0.04	-0.07	-0.45*
Mean temperature range	0.09	0.07	-0.05	-0.72*
Current variation	-0.24	-0.19	-0.16	-0.64*
Depth variation	-0.19	-0.23	-0.26	-0.67*
Spot stone movement	0.002	-0.04	-0.18	-0.59*
Mean stone movement	0.19	0.12	0.05	-0.57*
Pfankuch bottom component	0.12	0.15	-0.004	-0.46*
Tractive force	-0.01	-0.10	0.08	0.05
Overall stability	0.05	0.06	-0.05	-0.65*

a strong positive relationship was found between seasonal variation and stability ($F = 25.04, df = 1,7, P < 0.05$) (Fig. 3.12) provided Bruce Stream and Kowai River samples were removed from the analysis. Results obtained at these two sites were similar but appeared to be outliers with respect to the other data points.

Amount of organic material associated with the stone samples was correlated with a number of physical, chemical and stability measures (Table 3.6). The only stability measurement not negatively correlated with the stone organics was the percentage of substrate predicted to be moving, given the critical tractive force of the site.

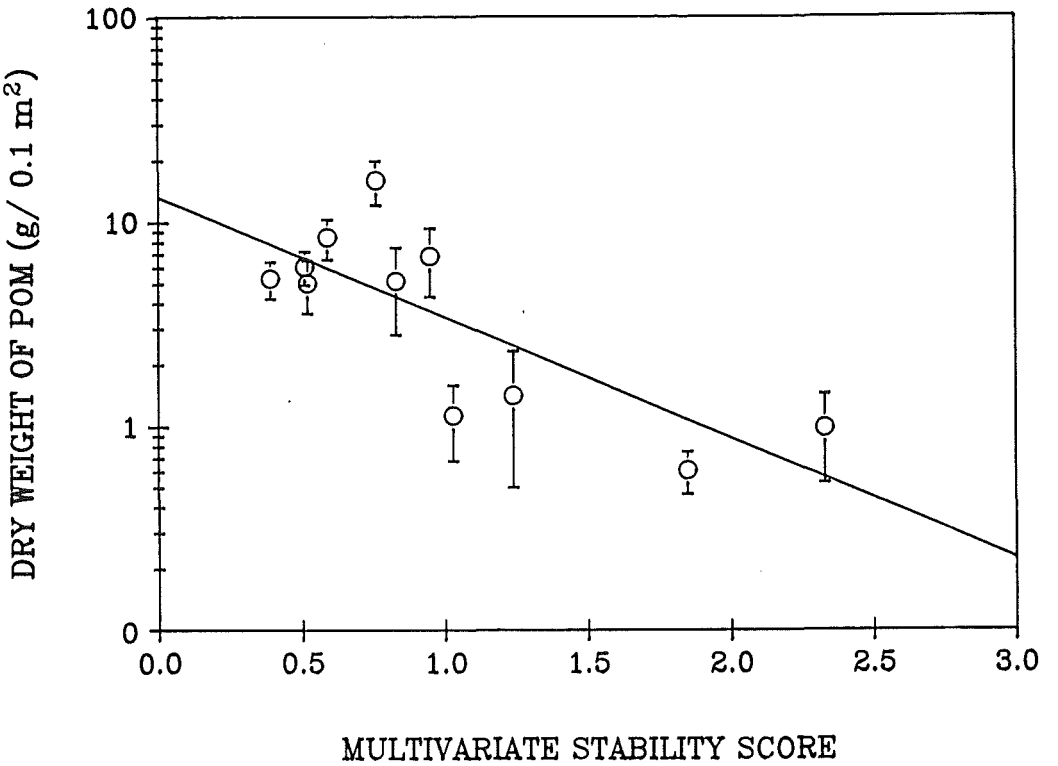


Figure 3.10. The relationship between the dry weight of particulate organic material associated with stones and overall stability. Plotted values are averages of the seasonal means ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, $\log_{10}$ (stone POM) = 1.04 - 0.69(stability score), r^2 = 0.50.

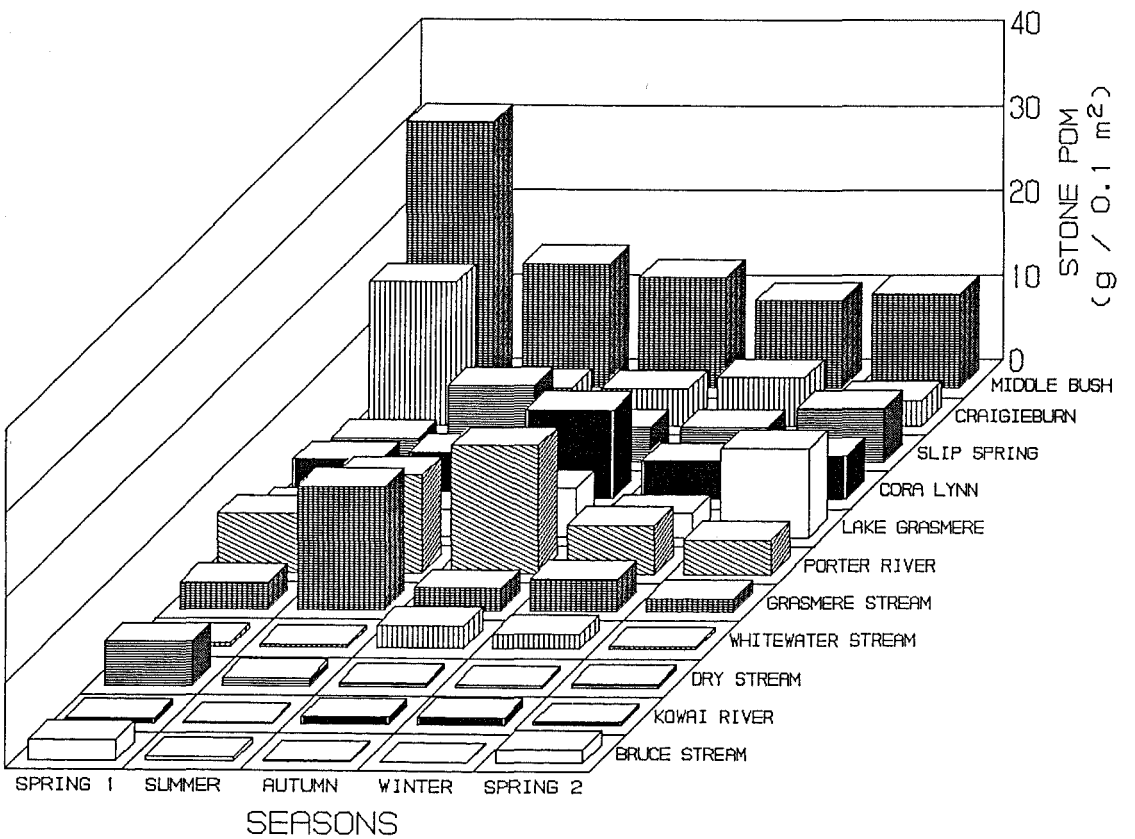


Figure 3.11. Mean dry weight of particulate organic material associated with stone invertebrate samples (n = 15) collected from the study sites between October 1987 and October 1988.

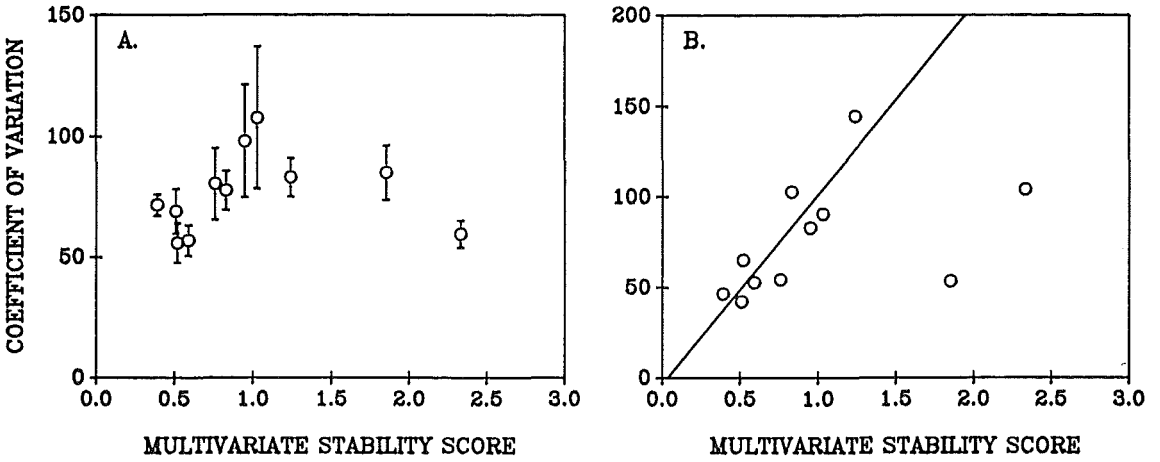


Figure 3.12. A. Mean (± 1 SE) of the coefficient of variation of particulate organic material associated with fifteen replicate stone samples (spatial variation) collected in each season at the study sites plotted against overall stability (multivariate stability score). The relationship was not significant, $r^2 = 0.07$.

B. Coefficient of variation of stone associated particulate organic material at the eleven study sites, based on mean values obtained in five seasons, plotted against overall stability. With all sites included the relationship was not significant, $r^2 = 0.19$. However with Kowai River and Bruce Stream (the two outliers) excluded a significant relationship exists (the plotted line); Seasonal CV = 104.8(stability score) - 3.82, $r^2 = 0.78$.

DISCUSSION

Both periphyton pigment concentrations and epilithic carbon concentrations were affected by overall environmental stability. With both variables exhibiting a logarithmic decline in concentration as stability decreased. All of the individual stability measurements were negatively correlated with these variables, and although other physical and chemical variables were correlated, these correlations were never as strong. Of all the measured physicochemical and stability variables the Pfankuch bottom component was the single best predictor in all but one case (epilithic carbon concentrations in the spring 1 sample, when mean stone movement was most important). In these small, nutrient poor streams it appears therefore that stream bed stability is the primary factor influencing the biomass of epilithon.

Seasonality in organic biomass on stone surfaces also appeared to be affected by the stability of a site, although different patterns were found for periphyton and epilithic carbon. Periphyton biomass at the unstable sites followed the classical textbook pattern of peaks in spring and lows in the winter, however, at stable sites peaks occurred in winter or autumn. Results obtained by Rounick & Gregory (1981) in an Oregon stream, suggested that the classical pattern of high periphyton biomass in spring and low biomass in winter was related to the higher frequency of flood events in winter removing periphyton by scouring. Thus, during a year of low

flows they found that periphyton biomass peaked in winter. This was the condition that occurred at my stable sites where severe winter flooding did not occur. Perhaps lower invertebrate grazing pressure during winter allows higher periphyton biomass to develop despite decreased light availability. Because stable and unstable sites responded differently to seasonal influences this also meant that the relationship between periphyton biomass and stability changed between the seasons.

In contrast to periphyton biomass (i.e., total pigment concentration) epilithic carbon concentrations peaked in autumn at the unstable sites and in spring or summer at the stable sites. Why total organic carbon should respond differently is difficult to explain, especially considering that the SEM study revealed that algae were a dominant component of the stone surface layers. Although Cowie (1980) has also found that the algal and non-algal components of epilithic communities in Middle Bush Stream respond differently to seasonal influences. My results seem to reflect a greater sensitivity of the non-algal component of the epilithon to substrate movement brought about by increased flows. The last two collections (winter (July) and spring 2 (October)) were preceded by two major spates in May and September, respectively, that affected all but a few of the sites. So, although algal biomass appeared to recover before samples were collected, two and one month later, respectively, total epilithic carbon had not recovered to the same extent.

In general, neither spatial nor seasonal variability of either of these parameters was related to the stability of a site. The one exception was the seasonal variability of periphyton biomass, which showed a marked increase with decreasing stability.

Similarly, stability appeared to have no major effect on periphyton community composition and in general the same taxa (blue green algae, *Gomphonema, Achnanthes lanceolata* and *Cocconeis*) predominated at all sites. Rather, stability appeared to effect periphyton biomass, such that the most obvious difference in the nature of stone surface communities between the two site groups was that those from the unstable sites were predominantly bare and any attached algae were found in crevices on the stone surfaces. In contrast, stone surfaces at the stable sites were covered with dense uniform mats of diatoms and blue green algae. There was also a greater diversity of diatom taxa at the stable sites. *Synedra, Cymbella, Gomphoneis*, filamentous diatoms and filamentous green algae also appeared to be more characteristic of the stable sites or stable periods of flow.

Quantities of particulate organic material collected in core samples were not related to any stability measurements made in these streams, but appeared to be related more to the size of stream and the nature of the overhanging vegetation. The forested streams, not surprisingly, contained the greatest amount of material despite being of intermediate stability. In contrast, amounts of particulate organic

matter collected in association with stone samples were strongly correlated with stability, decreasing as a site became more unstable. Why these two similar variables should have different relationships with stability is difficult to explain, but in part it probably reflects differences in the nature of this organic material. At several of the sites the organic material collected in association with stones was primarily moss and filamentous algae growing on the stone surfaces, whereas the material in core samples was primarily dead terrestrial plant material that had filtered down amongst the substrata. It is not surprising therefore, that amounts of stone associated organics were positively correlated with stability, as moss and filamentous algae both require relatively stable flow conditions.

In summary, environmental stability had a strong influence on the amount, and to a certain extent the type, of material present on stone surfaces. However, in the open streams at least, it did not appear to affect retention of organic material within the substrate.

INVERTEBRATE COMMUNITIES

INTRODUCTION

In this section I investigate a number of hypotheses concerning the influence of environmental stability on the community organisation of stream invertebrates. They include the influence of environmental stability on diversity patterns (Chapter 5), species-abundance distributions (Chapter 6), community composition (Chapter 7), community stability (persistence) (Chapter 8), community stability (resilience) (Chapter 9), competition (Chapter 10), and overlap of spatial resource utilization (Chapter 11). These chapters are based on samples collected at my study sites between October 1987 and October 1988 as detailed in Chapter 4. A summary of the data is presented in Appendix I.

CHAPTER 4

SAMPLE COLLECTION

SAMPLING RATIONALE

One of the principal questions addressed in this study is what influence does environmental stability have on community stability and complexity? Classically, this has involved examining the trophic structure of a community, and how the complexity of its structure affects its stability. Much of the theory, however, relates to the intensity of interaction between species in a community irrespective of whether interactions are associated with food or another resource. Competition for food (e.g., McAuliffe, 1984a; Hawkins & Furnish, 1987) and space (e.g., McAuliffe, 1984b; Hart, 1985; Hemphill, 1988) have both been shown to occur in stream invertebrate communities. Space therefore is likely to be an equally important resource to stream invertebrates, and consequently may also be an important factor in community organisation.

Competition for food resources may also lead to a separation of competing species in space and/or time. For example, Dudley *et al.* (1990) found that *Blepharicera micheneri* and *Simulium virgatum* occupied separate patches within the same Californian stream as a result of competition for food. Optimal foraging theory also predicts that predators and their prey will occur together (Krebs, 1978). Therefore, the occurrence or lack of occurrence of two species together (depending on the nature of their relationship) at a single point in space and time, may not only reflect the result of competition for spatial resources but may also reflect trophic interactions. A measure of spatial interaction may therefore in fact be a better representation than trophic interaction of the overall degree of interaction between two species (see Chapter 9 for a fuller discussion).

To measure the degree of spatial interaction of invertebrates in my study communities it was necessary to sample spatial resource states, and examine the degree to which their usage overlapped between species. This in itself is difficult, for how do stream invertebrates perceive spatial resources? An aquatic invertebrate may see a crevice in a rock surface as a completely different resource from a smooth exposed rock surface.

A fundamental constraint however, on any attempt to sample resource states is the degree to which they can be reliably sampled. I decided to use stones as naturally occurring environmental units, that could be reliably sampled, and between which spatial overlap could be measured. Stone samples also seemed to be

an appropriate scale for this study, because if spatial resource partitioning does take place, division of resources is likely to occur at boundaries between resources; the well defined edges of a stone are natural and highly probable boundaries for any such partitioning. The technique of measuring niche (or interaction) parameters over naturally occurring environmental units (such as stones) has received both theoretical support (Colwell & Futuyma, 1971; Allan, 1975; Hanski, 1978; Hurlbert, 1978; Hutchinson, 1978; Yodzis, 1978) and also support from field investigations involving aquatic invertebrates (Allan, 1975; Bruns & Minshall, 1983).

Finally, Wrona *et al.* (1986) proposed a technique for sampling benthic invertebrates using stones as sampling units, where both densities and their associated error terms are expressed in units of area of stream substrate. They claimed that their technique was superior to more conventional area-delimited sampling (e.g., Surber sampling) because it allows for variation resulting from both habitat heterogeneity and organism dispersion. Stone sampling, therefore, not only allows measurement of spatial overlap but may also provide a more efficient technique for measuring benthic invertebrate densities.

SAMPLING EFFICIENCY

The efficiency of the stone sampling technique was assessed against the more conventional, Surber sampling technique, and also enabled me to evaluate how many stones to collect at each site to obtain a relatively accurate estimate of population densities.

My comparison of the two techniques was carried out at the relatively stable Porter River site where there was a high density and diversity of invertebrates. Five random stone samples (a stone sample comprises three stones, one from each size class) and five random Surber samples were collected from the same stretch of stream. The collection nets used for the stone samples and forming part of the Surber sampler were 250 μm mesh. Samples were preserved in 10% formalin, sorted and identified to the lowest possible taxonomic level (see below for more details on sampling protocol).

The cumulative number of species collected in random combinations of samples are plotted in Fig. 4.1. Both techniques appeared to plateau at the five sample mark, indicating that few additional species would be collected with additional sampling. The Surber sampling technique appeared to collect consistently fewer species, however. This may be related to differences in sampling protocol between the two techniques. The Surber samples are obtained by disturbing the

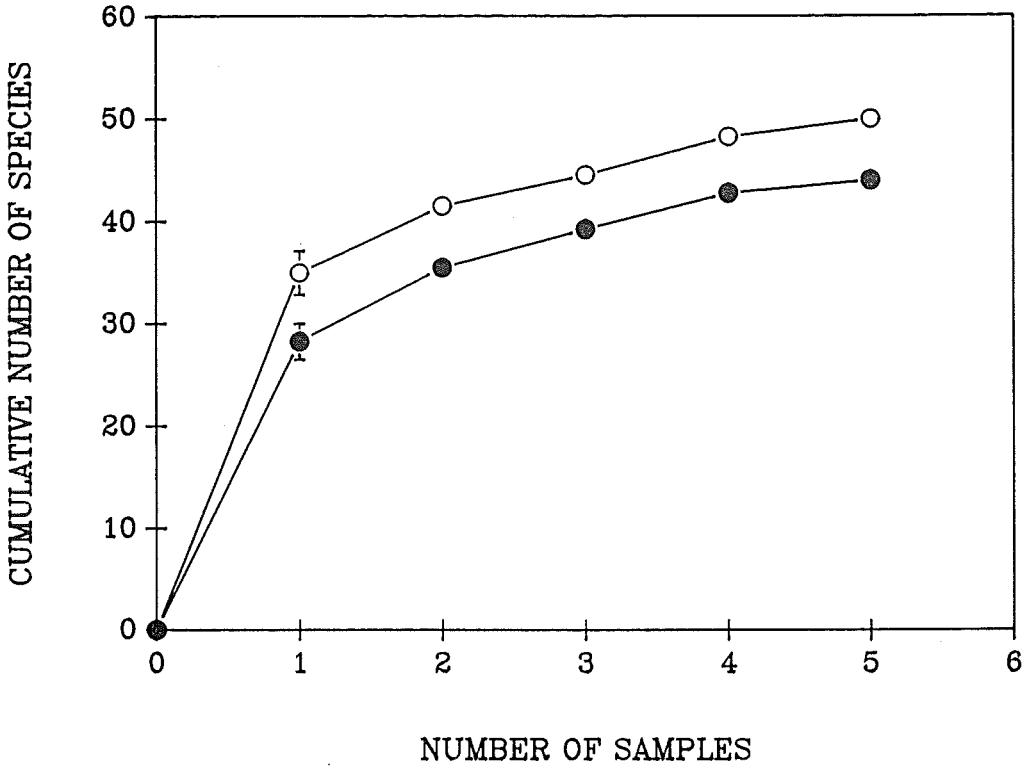


Figure 4.1. Mean cumulative number of species (± 1 SE) collected in random combinations of five stone (o) and Surber (•) samples.

substrate and collecting any dislodged animals in a net; a procedure that does not remove all the animals associated with the substrate (see Chapter 12). However, the stone sampling technique allowed the entire stone to be removed from the substrate and all the animals associated with it removed.

The density estimates for a number of taxa and their associated confidence intervals, obtained with both techniques are given in Table 4.1. Density estimates for the common invertebrates taken by both techniques appeared to be comparable (all T values indicated no significant difference between the two estimates, $P > 0.05$). Although intersample variability was slightly higher for the Surber samples (the average 95% confidence interval for the mean density of common taxa was ± 55% for Surber samples and ± 41% for stone samples). Elliot (1977) claimed density estimates with a standard error ± 20% of the mean was an acceptable precision for most ecological work and both techniques are approaching this level.

To improve the precision of density estimates obtainable by sampling stones to the point where estimates would have 95% confidence limits within ± 20% of the mean would have entailed collecting between 3 and 6 times as many samples. The considerable amount of extra sampling effort required to achieve this did not seem warranted given the small increase in accuracy that would result.

To further ensure that I was not missing species by sampling single stones, I

Table 4.1. Mean density estimates and 95% confidence intervals for those estimates using both Surber samples and stone samples for a number of rare and common taxa at Porter River. 95% confidence intervals are expressed as a percentage of the mean.

Taxa	Stone sample density estimate ($0.1\ m^{-1}$)	Surber sample density estimate ($0.1\ m^{-1}$)	Stone sample 95% confidence interval (±%)	Surber sample 95% confidence interval (±%)
Potamopyrgus antipodarum	708	466	40	49
Deleatidium sp.	278	351	34	22
Austrosimulium laticorne	837	125	54	75
Maoridiamesa harrisi	517	321	47	72
?Rheocricotopus sp.	93	24	45	124
Eukiefferiella claripennis	6	5	25	102
Hydrachenellae sp. A	7	20	100	65
Notoaturinae sp. A	18	32	43	72
Total	2861	1607	28	21

collected extensive "kick net" samples (250 μm mesh net) in association with the first seasonal samples. Sampling covered as wide a range of microhabitats within the sampling area as possible including any large boulders present, interstitial stone spaces, and stream edge margins. Between one and eighteen additional species were collected at the study sites by "kick sampling". However, none of the collected species was represented in these samples by more than 10 individuals, and in general only one or two individuals of each were collected. These rare species were unlikely to have had much impact on community organisation.

In summary, the stone sampling technique appeared to collect the majority of common species present within a study site. The accuracy of density estimates was moderate, but certainly no less accurate than those obtained from Surber samples.

SAMPLING PROTOCOL

Collections were made on 23 & 24 October 1987 (spring 1), 23, 24 & 25 January 1988 (summer), 23, 24 & 25 April 1988 (autumn), 23, 30 & 31 July 1988 (winter) and 23 & 24 October 1988 (spring 2). Fifteen random stones were sampled at each site, five stones from each of three size classes (large, maximum diameter 90-180 mm, medium, 60-90 mm and small, < 55 mm). These size classes correspond to the sizes of painted stones used to monitor substrate movement (Chapter 2).

Stones were sampled progressively as I moved upstream. A 250 μm mesh net was held behind each stone which was lifted rapidly into the net. Adjacent stones

were disturbed as little as possible but any fine sediment or detritus immediately below the stone was disturbed and any associated invertebrates were collected. Samples were preserved in 10% formalin.

Invertebrates larger than 1 mm body length were sorted by eye, whereas those 0.25 - 1 mm long were sorted out in a Bogorov tray at a magnification of x15. Two or three passes through the tray were made to ensure no animals were missed.

Where possible, invertebrates were identified to species level using the keys of Brinkurst (1971) (Oligochaeta), Chapman & Lewis (1976) (Crustacea), Ordish (1984) (Hydraenidae), McFarlane (1951) (Hydrobiosidae), Cowley (1978) (general Trichoptera), Cook (1983) (Acarina) and Winterbourn & Gregson (1989) (other aquatic taxa). However, the state of taxonomy of New Zealand aquatic invertebrates did not always allow this. Thus, although taxa could not always be named, they were still differentiated into apparent morphospecies.

Density calculations (and their associated error terms) were made with the technique of Wrona *et al.* (1986), which takes into account variation arising from both the heterogeneity of the habitat and the spatial dispersion of organisms.

Thus population density (d) = $\sum_{i=1}^{k} y_i.\bar{x}_i$

where d = the mean density of organisms (per unit habitat),

y_i = the stone weighting factor for the ith stone size class,

x_i = the mean number of organisms per stone in the ith stone size class

and k = the total number of stone size classes.

The variance of this density estimate is given by:

$$V(d) = \sum_{i=1}^{k} V(y_i.\bar{x}_i) + \sum_{i=1}^{k-1} \sum_{j=i+1}^{k} 2.COV(y_i.\bar{x}_i, y_j.\bar{x}_j)$$

where V(d) = the total variance of the weighted density estimate,

$V(y_i.\bar{x}_i)$ = joint variance of stone and mean organism estimates of the ith stone size class and

$COV(y_i.\bar{x}_i, y_j.\bar{x}_j)$ = the covariance correction between the ith and jth stone size classes.

The standard error of the estimated density is the square root of V(d). Density estimates were calculated per 0.1 m^2 of stream substrate, and stone weighting factors were assessed by examining the relative proportions of each of the three stone size classes in 10 random quadrats of 0.1 m^2. Actual calculations were performed using a Turbo BASIC program that I wrote.

CHAPTER 5

INVERTEBRATE DIVERSITY

INTRODUCTION

Attempts to explain spatial and temporal patterns of diversity in nature have been (e.g., Thoreau, 1860; Clements, 1916) and continue to be (May, 1986; Auerbach & Shimada, 1987) a pervading theme in ecological research. Many factors have been linked with observed patterns of diversity, including productivity, spatial heterogeneity, climatic variation, environmental harshness, environmental age, and disturbance, (both physical and biotic) (Pianka, 1983; Krebs, 1985; Begon *et al.*, 1990). Of these, the interaction between abiotic and biotic disturbances and diversity has been one of the most debated issues, with numerous equilibrium and nonequilibrium models put forward to explain observed patterns of diversity (for reviews see Thiery, 1982; Pickett & White, 1985; Petraitis *et al.*, 1989). However, the debate is still far from being resolved.

The link between disturbance and diversity in stream environments is also a dominant theme of research in stream ecology (Resh *et al.*, 1988), and several authors have postulated links between high diversity and increasingly stable environments (Minckley, 1963; Mackay & Kalft, 1969; Bishop, 1973; Cowie, 1980). In a number of studies a positive correlation has also been found between channel stability (as measured by the Pfankuch stability index) and species diversity (Rounick & Winterbourn, 1982, Winterbourn & Collier, 1987; Graesser, 1988). Flood events can also reduce density and diversity of invertebrate (Siegfried & Knight, 1977; Fisher *et al.*, 1982; McElravy *et al.*, 1989; Sagar, 1986; Scrimgeour & Winterbourn, 1989), periphyton (Tett *et al.*, 1978; Power & Stewart, 1987) and fish (Matthews, 1986; Meffe & Minckley, 1986) communities, at least initially. However, although it is clear that severe disturbances reduce diversity, the effects of lesser disturbances are unclear.

Equilibrium models have been suggested to explain patterns in benthic community structure (e.g., Minshall & Peterson, 1985), however, as in other areas of ecology (e.g., Strong *et al.*, 1984; Diamond & Case, 1986), there appears to be a general trend away from such models towards nonequilibrium models because of the stochastic nature of many environments (but see DeAngelis & Waterhouse, 1987 and Petraitis *et al.*, 1989). The intermediate disturbance hypothesis (Grime, 1973; Connell, 1978) may be a suitable model to describe diversity patterns in lotic systems, and until recently, has been the dominant hypothesis dealing with

diversity in stream ecology (Ward & Stanford, 1983; Resh *et al.*, 1988). It predicts that diversity will be greatest at intermediate levels of disturbance. In the face of little or no disturbance, it is hypothesized that competitive exclusion will be able to proceed towards equilibrium and diversity will decrease as competitively inferior species are eliminated. If disturbances are too severe or too frequent, on the other hand, resident species will be eliminated and replaced by others that are more efficient colonisers, but competitively inferior. At intermediate levels of disturbance both groups are able to persist and diversity peaks. This hypothesis has received support from both theoretical (Petraitis *et al.*, 1989) and empirical (Stanford & Ward, 1983) studies.

Investigations into the effects of disturbance on diversity are fraught with definition problems (Thiery, 1982; Petraitis *et al.*, 1989; Lake, 1990), and the intermediate disturbance hypothesis is no exception. Disturbance in the context of the hypothesis can be either biotic (e.g., predation) or abiotic (e.g., physical disturbance), but for the purposes of this study I am considering only purely abiotic disturbances. This in itself generates problems, for as environmental stability increases the impact of predation may also increase (Menge & Sutherland, 1976, 1987; Peckarsky, 1983; Peckarsky *et al.*, 1990) (but see Walde, 1986). The effect of predation on diversity also depends on the nature of the predator itself; if a major predator prefers the competitive dominant as prey, then increased predation pressure should enhance species diversity (e.g., Paine, 1966). However, if competitive dominants are not the preferred prey then in theory at least increased predation will result in decreased species diversity (e.g., Lubchenco, 1978). As the impact and mechanisms of predation *per se* in stream environments are still poorly understood, it is difficult to predict how the affect of predation may alter with increasing stability of the physical environment.

Experimental studies into the effects of disturbance on stream invertebrate communities (Clifford, 1982; Reice, 1984, 1985; Robinson & Minshall, 1986; Doeg *et al.*, 1989; Lake *et al.*, 1989) in general have not supported the intermediate disturbance hypothesis, although Malmqvist & Otto (1987) claim weak but inconclusive support for the concept. However, the methodology and scale at which these experiments have been conducted have been severely criticised by both Minshall (1988) and Lake *et al.* (1989). All have involved manipulation of small patches of stream or artificial substrata, and while they may mimic the effects of minor floods (Doeg *et al.*, 1989) they do not test the effects of disturbance on entire stream reaches, as proposed in Ward & Stanford's (1983) original application of the hypothesis.

In a recent review of the role of disturbance in stream ecosystems, Resh *et al.*

(1988) concluded that the applicability of the intermediate disturbance hypothesis is contingent upon demonstration of the generality of competitive hierarchies. These have been shown to occur in stream systems (e.g., McAuliffe, 1984a, 1984b; Hart, 1985; Hawkins & Furnish, 1987; Hemphill, 1988; Dudley *et al.*, 1990), but the generality of such relationships is far from conclusive (Reice, 1985). It is also necessary to demonstrate that a trade-off between superior competitive ability and the ability to colonise newly available habitat occurs (Petraitis *et al.*, 1989). Again there is some support for this idea. For instance, Hemphill & Cooper (1983) observed that larval *Simulium virgatum* which colonised bare stones following a disturbance were eventually replaced by the competitively dominant *Hydropsyche oslari* (Hemphill, 1988). Likewise, stream channels in England, colonised by adult midges from nearby streams, were initially dominated by a previously undescribed species of chironomid (*Orthocladius calvus*) (Ladle *et al.*, 1985; Pinder, 1985), but were eventually replaced by a more "normal" complement of chironomid species. In contrast, neither Reice (1984, 1985) nor Doeg *et al.* (1989) found evidence of a specialized "colonising" fauna in their experimental studies. Whether stream invertebrates exhibit any trade-off between competitive ability and colonising ability is clearly still uncertain and in need of further investigation.

Of the three major hypotheses that Resh *et al.* (1988) reviewed, Huston's (1979) dynamic equilibrium model was considered to be most generally applicable to stream communities. It models community structure as a trade-off between the frequency of population reduction and the rate at which competitive exclusion proceeds, and the latter in turn is related to the productivity of the environment. If the interval between disturbance events is shorter than the time required for competitive exclusion then initial diversity levels should be maintained. However, under conditions of infrequent disturbance an increase in population growth rates of strong competitors would lead to a decrease in diversity via competitive displacement. It is unclear, however, whether lower productivity would suppress competitive exclusion because population growth rates are depressed or enhance competitive exclusion because resources are more limiting (McGuinness, 1987). The question of how disturbance and productivity may be linked, and in turn how this effects competition still remains to be tested in stream environments. However, McGuinness (1987) has rejected Huston's model as an explanation of community patterns in intertidal boulder communities.

Hypotheses, such as the equal chance hypothesis (Connell, 1978; Sale, 1977, 1980a), have also been suggested as worth considering to explain patterns in stream community structure (Hart, 1983; Lake, 1986), but have received little support.

The exact nature of the relationship between diversity and disturbance in stream environments therefore remains essentially unresolved, and future attempts to examine the problem, must resolve problems of both definition and scale. Thus, Reice (1984, 1985) and Robinson & Minshall (1986) found that species richness and what they termed diversity (this was actually the Shannon-Wiener index of diversity) responded differently to disturbance. This illustrates one of the fundamental difficulties in studies of diversity, principally that there are two components to diversity, species richness and species evenness, which do not necessarily respond to disturbances in a similar way. Hurlbert (1971) even went so far as to suggest that diversity was a non-concept because of the problems involved in defining and measuring it. In this chapter I examine both components of diversity separately and consider their relationships with six separate measures of environmental stability, and a combined stability measure encompassing all six variables.

MATERIALS AND METHODS

A large number of indices are available for assessing species diversity, each one with it's own advantages and disadvantages. These indices have variously been reviewed by May (1975), Pielou (1975), Southwood (1978), Washington (1984), Ludwig & Reynolds (1988) and Magurran (1988) to name a few. Despite having been extensively reviewed there is still little concensus as to which measure or measures are best. The choice of an index is further complicated by the fact that diversity comprises two components, species richness (i.e., the number of species) and species evenness or equitability (i.e., how the individuals are distributed amongst species). Although some indices combine both components, this may in fact obscure much potentially useful information.

I chose to use several indices, each measuring a slightly different aspect of diversity. They are all simple indices that are easy to interpret biologically, and have received consistent support in reviews on the topic. The indices are:

1. Species number (S).

2. Margalef's index (Clifford & Stephenson, 1975), a simple measure of species richness given by:

$$D_{Mg} = (S-1)/\ln N$$

where N = the total number of individuals collected.
Its use is advocated by Magurran (1988) among others.

3. The log series alpha index (Taylor, 1978) which is also essentially a measure of species richness and is given by:

$$\alpha = \frac{N(1-x)}{x}$$

where x is estimated from the iterative solution of:

$$S/N = (1-x)/x[-\ln(1-x)].$$

The properties of this index have been investigated thoroughly (Taylor, 1978; Kempton & Taylor, 1974, 1976) and it is recommended by several authors (Taylor, 1978; Southwood, 1978; Magurran, 1988) because of its good discriminating ability and relatively low dependence on sample size. It remains a satisfactory measure of diversity even when the underlying species-abundance distribution is not a log series (Taylor, 1978), although in my case, most data sets did fit such a distribution (see Chapter 6). Shepard (1984) recommended it as an appropriate index for describing stream benthic communities, because the assumptions of the log series distribution seemed particularly appropriate for samples of benthic invertebrates.

4. The Berger-Parker dominance index (Berger & Parker, 1970), which is a simple measure of evenness (or dominance) given by:

$$D = N_{max}/N$$

where N_{max} = the number of individuals in the most abundant species and
N = the total number of individuals collected.

It is an intuitively simple index advocated by May (1975) and Magurran (1988) as an index of dominance.

5. Simpson's index (1949), which is also a measure of evenness and has the form:

$$D = \sum \frac{(n_i(n_i-1)}{(N(N-1))}$$

where n_i = the number of individuals in the ith species and
N = the total number of individuals collected.

This index is strongly weighted towards the most abundant species, but is advocated by a number of authors including May (1975) and Washington (1984), because it better reflects the entire species-abundance distribution than other similar indices (e.g., the Shannon-Wiener index).

The last two indices were expressed as reciprocals so that, as for the other indices, an increase in the index represents an increase in that diversity component.

It is worth noting here that in many studies of disturbance the Shannon-Wiener index, H' (which is based on information theory) has been used as a diversity measure. However, its biological relevance has been severely criticised by Hurlbert (1971), Goodman (1975) and May (1975) to name a few, and is held by many as an inappropriate measure of diversity. Consequently, I have not used this index, despite its rather widespread use.

ANALYSIS

Data were analysed with the regression, stepwise regression and Spearman rank correlation procedures of SAS (1985). Stepwise regression of diversity variables was carried out using the 26 biological, chemical, physical and stability measurements listed in Table 5.1. Spot measurements are those made at the time of collection or for the month prior to the collection of samples. The critical probability for addition and removal of variables to the model was set at 0.05. The same variables were used in the correlation analysis.

RESULTS

A total of 185 species were collected in the seasonal sampling program with any one collection (i.e., all the stones collected in each season at a site) containing between 7 and 64 species. The number of species taken at each site is shown in Fig. 5.1. This decreased as the overall environmental stability (i.e., the multivariate stability scores) of the site decreased (Fig. 5.2) (F = 136.66, df = 1,49,

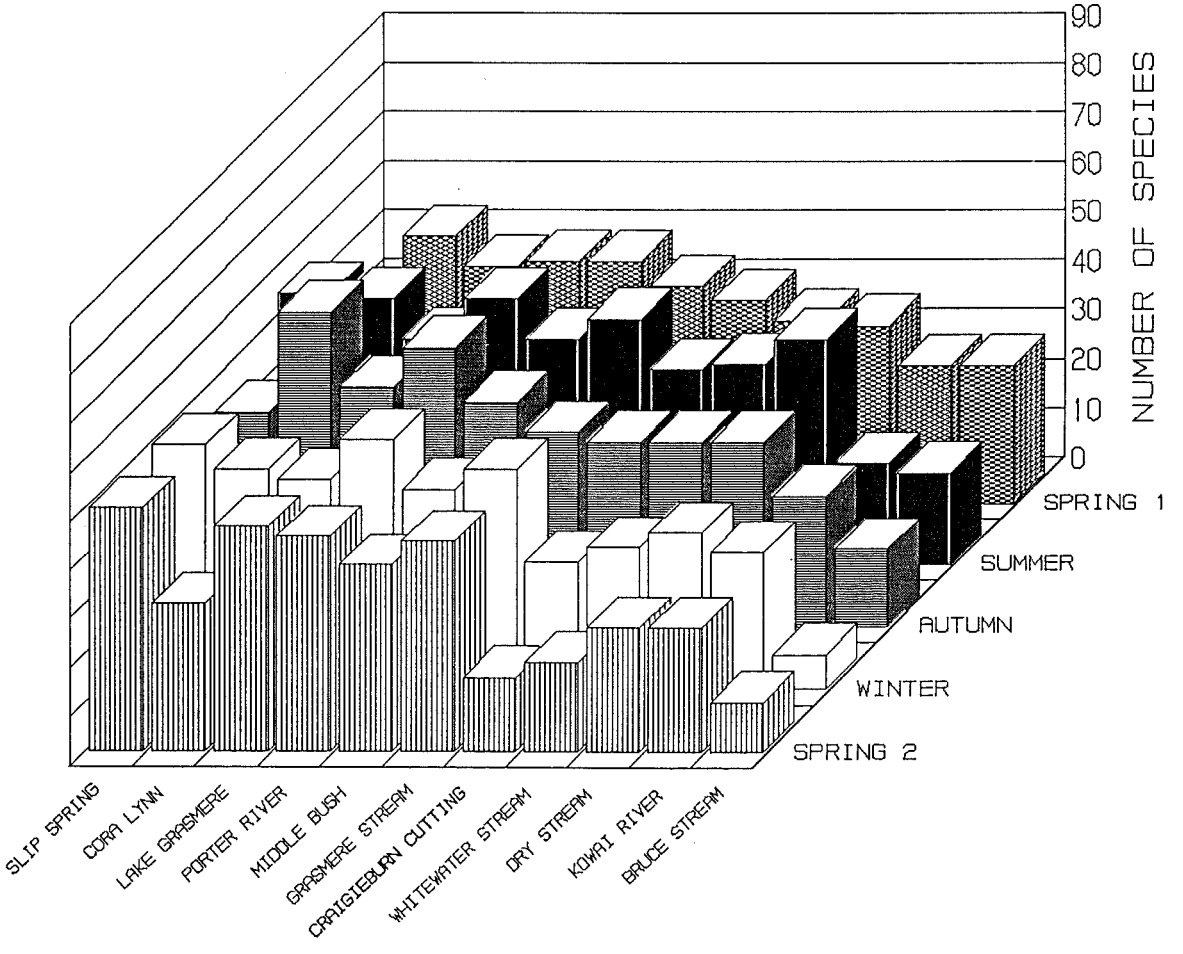


Figure 5.1. Total number of species collected in each season at the study sites between October 1987 and October 1988.

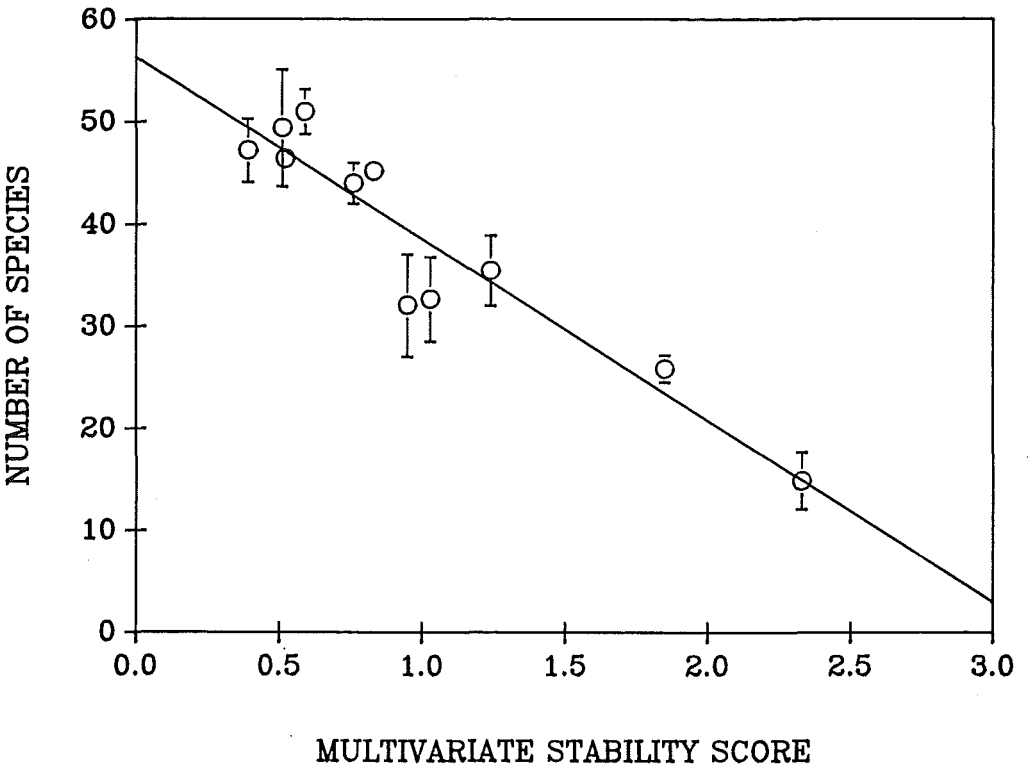


Figure 5.2. Number of species as a function of overall stability (multivariate stability score). Plotted values are the averages over all seasons of the total number of species collected on each sampling date at a site ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, number of species = 49.03 - 17.76(stability score), r^2 = 0.77.

$P < 0.05, r^2 = 0.77$). The number of species collected was also significantly different between the seasons ($F = 5.92, df = 4,49, P < 0.05$), although this difference existed primarily between the spring 2 sample and the others. Significantly fewer species occurred in spring 2 than in all the other seasons except winter (the only other significant difference in species number was between winter and summer). Lower species numbers in spring 2, and to a lesser extent winter, was probably the result of an increase in the size and severity of spates during these seasons when even some of the more stable sites (especially Cora Lynn and Middle Bush) were mildly disturbed.

The nature of the relationship between the number of species and the stability of a site (i.e., the slope of the graph) did not change with season, however ($F = 0.49, df = 4,45, P > 0.05$). This was surprising given that during these latter two seasons (i.e., spring 2 and winter) conditions in many of the streams were considerably more unstable than at other times of the year. During such periods one might have expected the more unstable sites to be more severely affected by increases in disturbance, than the stable sites. If so, the slope of the regression should become progressively steeper, i.e., the more unstable sites should lose proportionally more species, because they experience more severe disturbances.

Examination of Fig. 5.3, however, indicates that the sites at either end of the regression line were maintaining proportionally similar numbers of species, and that only the sites of intermediate stability were falling below the regression line.

When the relationship was examined using average stone movement at a site as the measure of stability, rather than the multivariate stability scores, the same

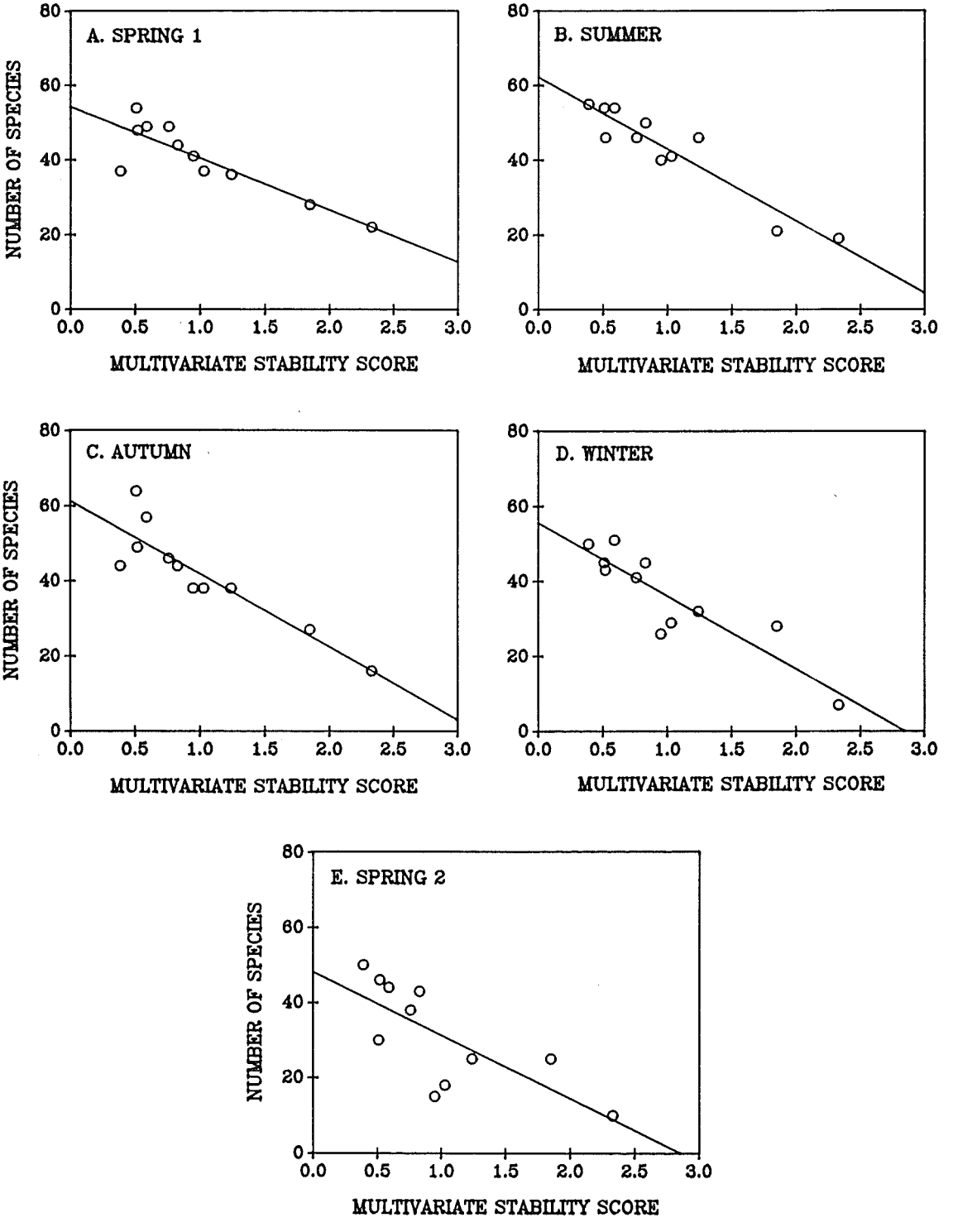


Figure 5.3. Total number of species collected in each season as a function of overall stability (multivariate stability score).

overall pattern emerged (Fig. 5.4). However, the positions of the sites of intermediate stability changed, and rather than simply dropping below the regression line they fell away in a linear manner (dotted lines) so that the slope of the relationship between stability and species number increased (F = 3.85, df = 4,35,

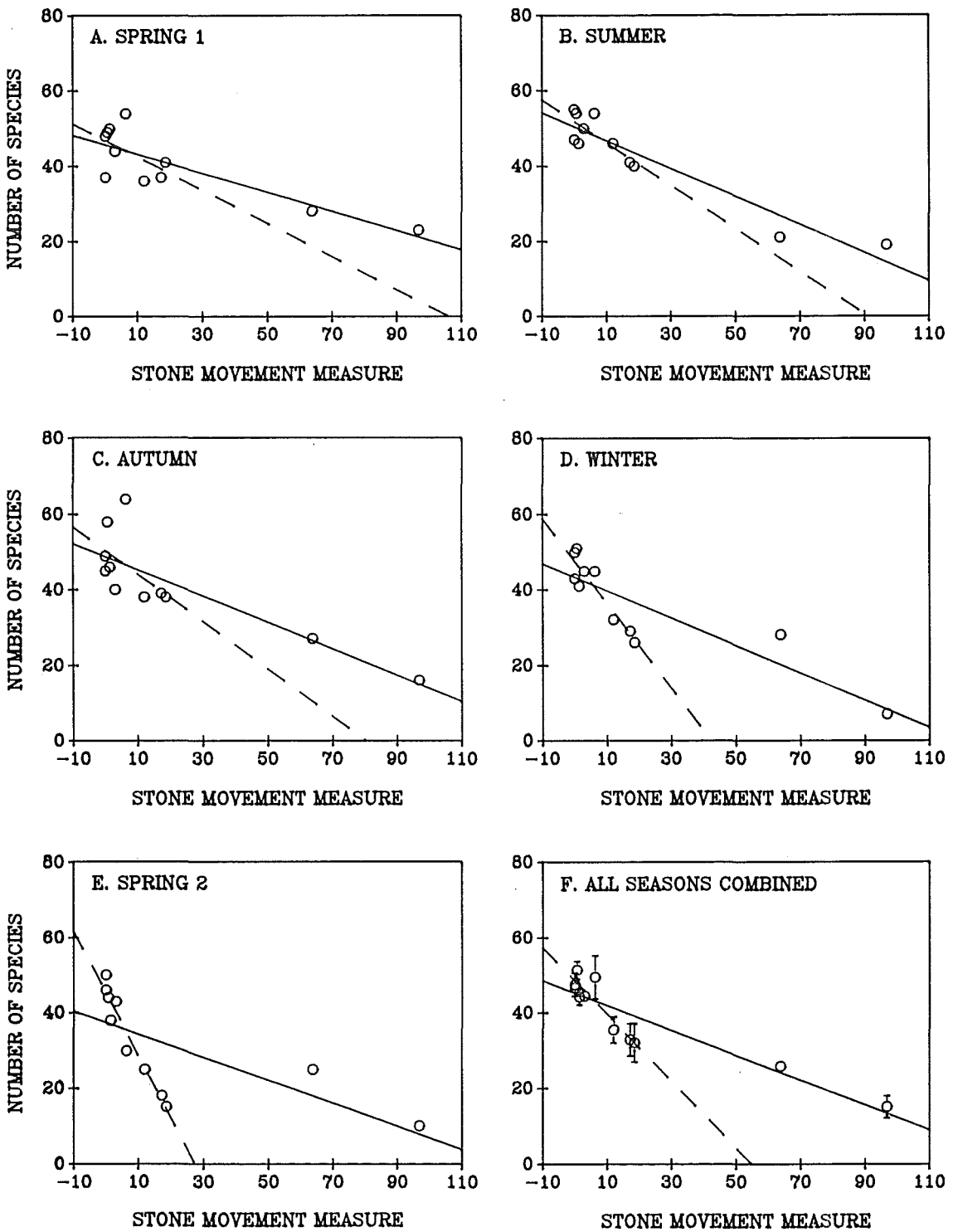


Figure 5.4. Total number of species collected in each season as a function of mean stone movement, and for the seasons combined. Regressions with solid lines include Kowai River and Bruce Stream in the analysis, those with dashed lines are regressions excluding these two sites.

$P < 0.05$); the predicted response. The two most unstable sites (Kowai River and Bruce Stream) again did not show a proportionally greater decrease in species numbers in the face of increased disturbance and therefore the slope of the regression incorporating all sites did not increase. In fact, the number of species at these highly unstable sites appeared to be unaffected by increasingly unstable conditions, and it was only the sites of intermediate stability that showed a distinct reduction in species number in response to increased disturbances (Note however, that the effect of increased disturbances on diversity at the most stable sites was not examined, as these sites experienced little or no increased disturbance).

The total number of animals collected from the fifteen stones at each site in any one season ranged from 16 at Bruce Stream to 16,047 at Slip Spring (Fig. 5.5). Seasonal patterns in the total number of animals appeared to be similar in both stable and unstable sites with peaks of abundance in the first spring and summer. These seasonal differences were significant ($F = 4.41$, $df = 4,49$, $P < 0.05$), with spring 1, summer and autumn having significantly higher densities than winter and spring 2, probably because many of the streams experienced more unstable conditions during these latter two seasons. Similarly, across all the seasons, total

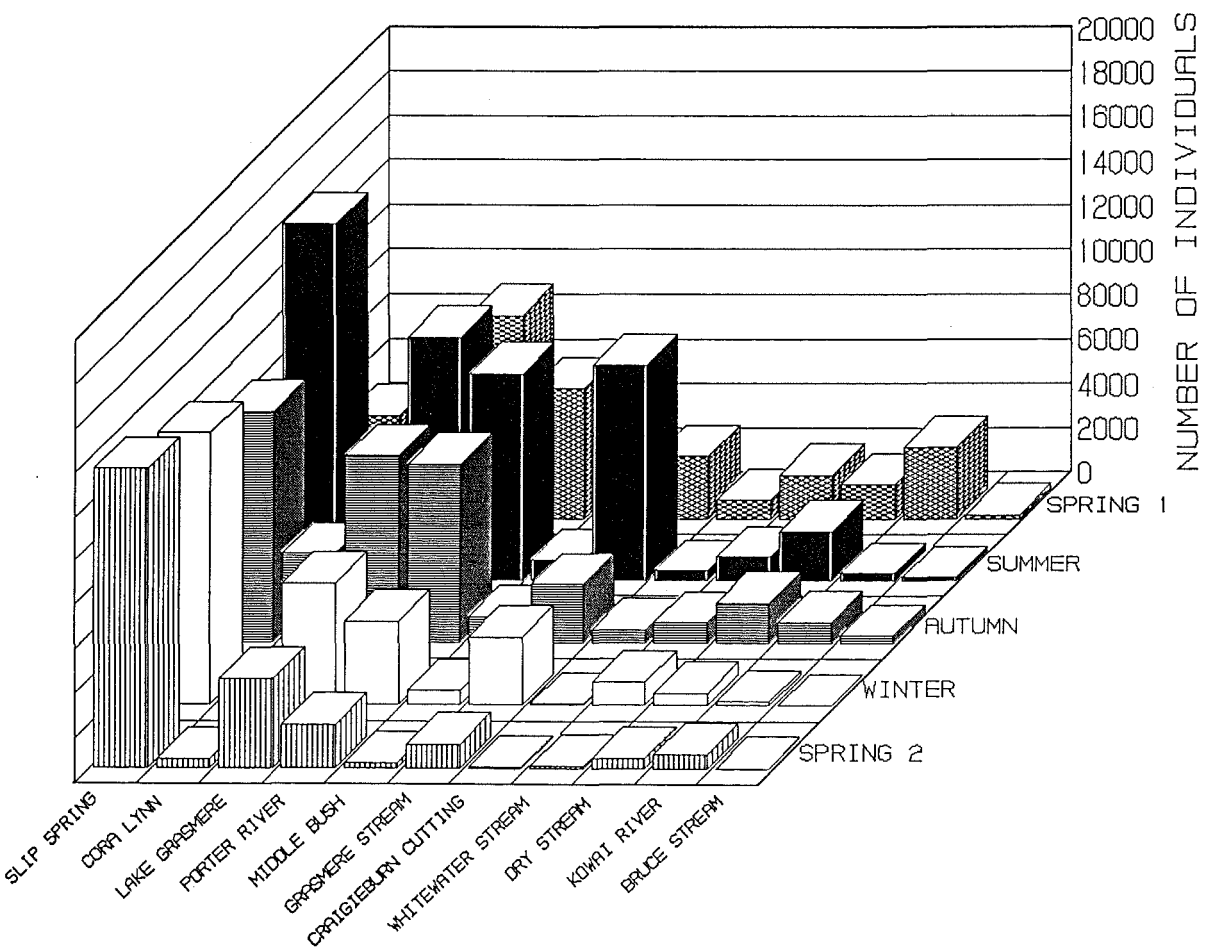


Figure 5.5. Total number of individuals collected in each season at the study sites between October 1987 and October 1988.

number of invertebrates was considerably lower in the less stable sites (Fig. 5.6) (F = 57.90, df = 1,49, P < 0.05, r^2 = 0.61) with a similar relationship between overall stability and total number of animals in all the seasons (F = 0.93, df = 4,45, P > 0.05).

Seasonal variation in the number of species (i.e., the coefficient of variation of the five seasonal samples) (Fig. 5.7) was not significantly related to stability (F = 3.23, df = 1,9, P > 0.05, r^2 = 0.26). However, if the relatively invariable Kowai River data are omitted, a significant increase in seasonal variability is found with a decrease in environmental stability (F = 7.89, df = 1,8, P < 0.05 r^2 = 0.50). Thus, in general the unstable sites showed a greater proportionate change in the total number of species between each of the seasons. Similarly, the relative change in the total number of individuals between seasons (i.e., the coefficient of variation of the five seasonal samples) (Fig. 5.7) increased with a decrease in stability (F = 8.37, df = 1,9, P < 0.05, r^2 = 0.48).

Both numbers of species and total numbers of individuals were correlated with similar variables (Table 5.1). They were both positively correlated with epilithic pigment concentration, epilithic carbon concentration, and stone associated

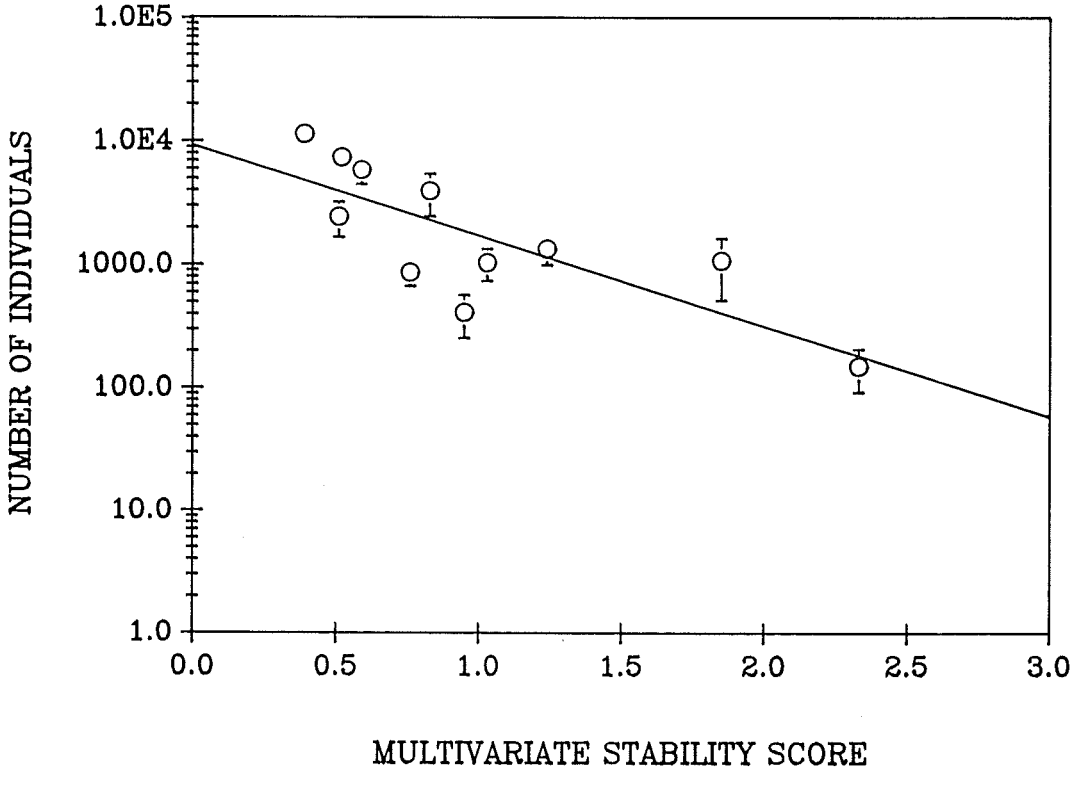


Figure 5.6. Total number of individuals as a function of overall stability. Plotted values are the averages over all seasons of the total number of individuals collected on each sampling date at a site ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, $\log_{10}$ (total number) = 3.55 - 0.82(stability score), r^2 = 0.61.

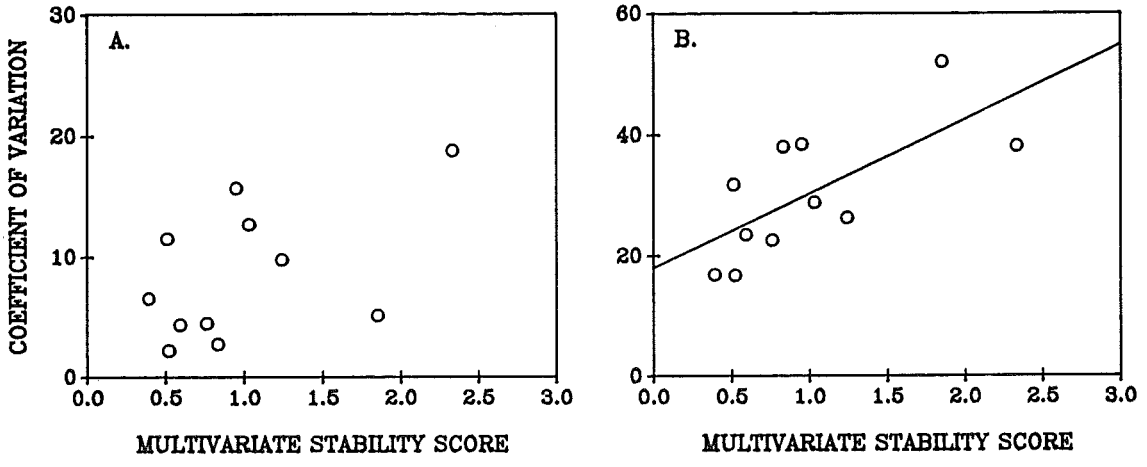


Figure 5.7. Coefficient of variation of number of species (A) and total number of individuals (B), over the five seasons as a function of overall stability. The regression analysis for the number of species was not significant (r^2 = 0.26), however, that for the number of individuals yielded the equation, seasonal CV = 17.92 + 12.31(stability score), r^2 = 0.48.

POM biomass. With the exception of tractive force (which was not correlated with species number) both were also negatively correlated with all stability measures. Spot water temperature and spot current velocity readings were also significantly related to both variables.

In a stepwise regression analysis the overall stability score was the single best predictor of the number of species at a site in all but one of the seasons (spring 2) (r^2 = 0.75-0.88) and for all seasons combined (r^2 = 0.65) (Table 5.2). In spring 2 epilithic carbon concentration was the best predictor (r^2 = 0.60). Total numbers of individuals at a site were best predicted by epilithic pigment concentration in each of the seasons (r^2 = 0.81-0.90) and for all seasons combined (r^2 = 0.63) (Table 5.3).

The response of the diversity indices to stability essentially fell into two categories corresponding to species richness and species evenness/dominance. The two indices of species richness, Margalef's index and the log series alpha index, both showed a significant decrease with a decrease in stability (Fig. 5.8) (F = 52.66, df = 1,49, $P < 0.05$, r^2 = 0.54, and F = 11.16, df = 1,49, $P < 0.05$, r^2 = 0.22 for Margalef's index and the log series alpha index, respectively). In contrast, both the evenness indices, the Berger-Parker dominance index and Simpson's index, showed no significant linear relationship with stability (Fig 5.8) (F = 3.34, df = 1,49, $P > 0.05$, r^2 = 0.08, and F = 3.38, df = 1,49, $P > 0.05$, r^2 = 0.07 for the Berger-Parker index and Simpson's index, respectively). These two indices although not related linearly to stability, did however, reveal interesting patterns. Maximum diversity (i.e., minimum dominance) was exhibited by

Table 5.1. Correlation (r_s) of several diversity measures with a number of biological, hydrological and chemical parameters. The hydrological and chemical parameters were monthly measurements made at the study sites between October 1987 and May 1989, and the biological parameters were those collected in association with the invertebrate samples (see Chapters 2 and 3). * indicates significant correlations at $P = 0.05$.

Physicochemical/ Biological parameter	Species number	Total number of individuals	Margalef's index	Log series alpha index	Berger-Parker dominance index	Simpson's index
BIOLOGICAL						
Epilithic pigment conc.	0.72*	0.83*	0.23	0.04	0.11	0.07
Epilithic carbon conc.	0.79*	0.81*	0.38*	0.20	0.19	0.18
Coarse POM	-0.08	-0.18	0.20	0.25	0.08	0.11
Fine POM	0.03	-0.15	0.23	0.22	0.06	0.07
Total POM	-0.10	-0.24	0.20	0.25	0.04	0.08
Stone POM	0.70*	0.42*	0.72*	0.63*	0.46*	0.49*
CHEMICAL						
Spot conductivity	0.24	0.11	0.23	0.19	0.23	0.19
Spot pH	0.17	0.01	0.23	0.20	0.31*	0.22
Mean Conductivity	0.21	-0.05	0.33*	0.31*	0.28*	0.32*
Mean pH	0.11	0.03	0.14	0.12	0.20	0.14
Mean alkalinity	0.46*	0.26	0.38*	0.29*	0.21	0.30*
PHYSICAL						
Spot current velocity	-0.37*	-0.30*	-0.33*	-0.26	0.09	0.05
Spot depth	-0.22	-0.08	-0.39*	-0.37*	-0.002	0.02
Spot temperature	0.35*	0.36*	0.14	-0.02	0.23	0.15
Mean current velocity	-0.39*	-0.21	-0.49*	-0.47*	-0.14	-0.15
Mean depth	-0.24	-0.01	-0.53*	-0.56*	-0.17	-0.21
Mean temperature	-0.17	0.09	-0.37*	-0.35*	-0.03	-0.13
STABILITY						
Spot temperature range	-0.45*	-0.36*	-0.40*	-0.32*	-0.08	-0.17
Mean temperature range	-0.64*	-0.46*	-0.53*	-0.42*	-0.23	-0.34*
Current variation	-0.52*	-0.34*	-0.56*	-0.51*	-0.22	-0.21
Depth variation	-0.50*	-0.30*	-0.60*	-0.55*	-0.26	-0.31*
Spot stone movement	-0.67*	-0.71*	-0.38*	-0.22	-0.21	-0.19
Mean stone movement	-0.76*	-0.80*	-0.41*	-0.23	-0.26	-0.24
Pfankuch bottom comp.	-0.75*	-0.76*	-0.40*	-0.25	-0.14	-0.09
Tractive force	-0.15	-0.37*	0.07	0.11	-0.06	0.02
Overall stability	-0.77*	-0.71*	-0.51*	-0.37*	-0.15	-0.16

sites of intermediate stability, with very stable and unstable sites having a similar degree of evenness. A similar trend was also evident for the two indices of species richness, although it was not as pronounced, and the very unstable sites had a lower diversity than the very stable sites.

Correlation of species richness and evenness indices with physicochemical and biological variables also revealed two different patterns (Table 5.1). The two species richness indices were negatively correlated with most of the stability

Table 5.2. Results of a stepwise regression analysis of the number of species collected in each season at the study sites against 26 biological, physicochemical and stability measurements. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Parameter estimate	Partial r^2	Model r^2
SPRING 1			
Intercept	43.28		
Overall stability	-12.82	0.75	0.75
Mean conductivity	0.14	0.15	0.90
SUMMER			
Intercept	54.41		
Overall stability	-6.47	0.88	0.88
Current velocity variation	0.29	0.05	0.93
Spot stone movement	-0.28	0.03	0.97
Spot conductivity	0.10	0.02	0.98
Total POM	-8.99	0.01	0.993
Mean depth	-0.21	0.01	0.9988
Fine POM	-4.41	0.001	0.9998
AUTUMN			
Intercept	61.37		
Overall stability	-19.46	0.80	0.80
WINTER			
Intercept	55.61		
Overall stability	-19.52	0.81	0.81
SPRING 2			
Intercept	57.62		
Epilithic carbon conc.	1.19	0.60	0.60
Spot conductivity	0.10	0.16	0.77
Mean stone movement	-0.25	0.12	0.89
Total POM	-31.19	0.06	0.96
ALL SEASONS COMBINED			
Intercept	40.45		
Overall stability	-18.66	0.65	0.65
Epilithic carbon conc.	0.31	0.07	0.72
Stone POM	0.60	0.04	0.76
Current variation	0.44	0.03	0.79
Spot conductivity	0.06	0.02	0.81
Spot current velocity	-10.87	0.02	0.83

Table 5.3. Results of a stepwise regression analysis of the total numbers of individuals collected in each season at the study sites against 26 biological, physicochemical and stability measurements. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Parameter estimate	Partial r^2	Model r^2
SPRING 1			
Intercept	-1199.72		
Epilithic pigment conc.	1811.26	0.81	0.81
Spot conductivity	16.37	0.07	0.89
SUMMER			
Intercept	4233.07		
Epilithic pigment conc.	2119.16	0.88	0.88
Coarse POM	-3939.16	0.06	0.94
AUTUMN			
Intercept	2663.02		
Epilithic pigment conc.	947.33	0.89	0.89
Mean temperature range	-326.92	0.07	0.96
WINTER			
Intercept	24740.73		
Epilithic pigment conc.	687.01	0.90	0.90
Spot pH	-3307.70	0.07	0.97
SPRING 2			
Intercept	35592.60		
Epilithic pigment conc.	922.88	0.85	0.85
Mean pH	-4800.76	0.08	0.92
ALL SEASONS COMBINED			
Intercept	4195.46		
Epilithic pigment conc.	550.47	0.63	0.63
Epilithic carbon conc.	177.67	0.11	0.74
Mean conductivity	-39.14	0.05	0.78
Mean temperature range	-232.34	0.03	0.81

measures and several physical variables, including mean depth, current velocity and temperature, and positively correlated with several biological and chemical variables, including stone associated POM, conductivity and alkalinity. In contrast, the two evenness measures were poorly correlated with all variables except stone associated POM, with which they were positively correlated.

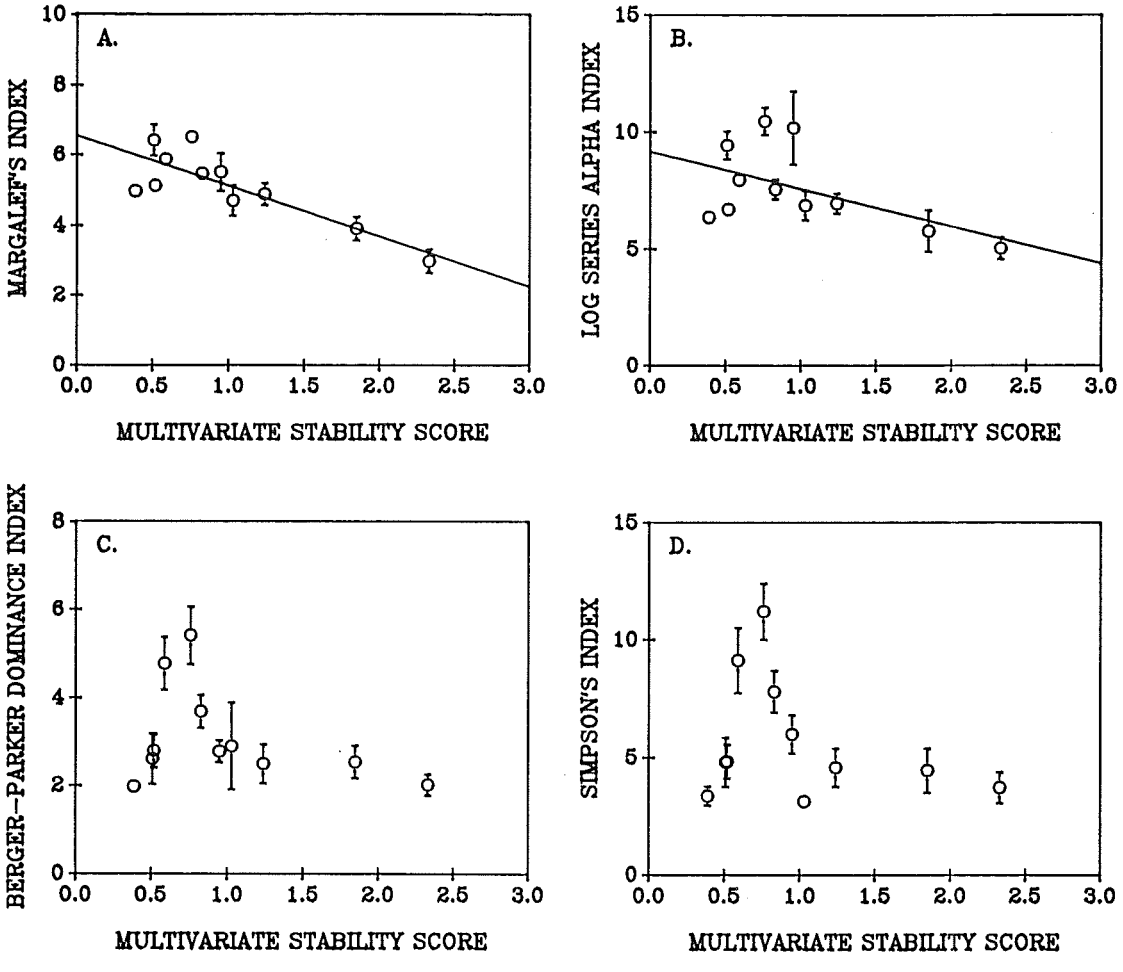


Figure 5.8. Margalef's index (A), log series alpha index (B), Berger-Parker dominance index (C) and Simpson's index (D) as a function of overall stability. Plotted values are the averages over all seasons of the index scores recorded on each sampling date at a site ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equations: Margalef's index = 6.07 - 1.44(stability score), r^2 = 0.54 and log series alpha index = 8.75 - 1.59(stability score), r^2 = 0.22. The Berger-Parker dominance index and Simpson's index both had nonsignificant regressions (r^2 = 0.08 and r^2 = 0.07, respectively).

Stepwise regression analysis of the indices was not particularly revealing. Significant predictors of each of the diversity indices were found to be inconsistent between seasons and many seasons had no significant predictors. Not even the single best predictor of each of the diversity indices was consistent between seasons. Multivariate regression models for the pooled data sets (i.e., all seasons combined) are given in Table 5.4. For Margalef's index the best predictor was mean stone movement, with mean conductivity, tractive force and stone associated POM also important (total r^2 = 0.70). For the log series alpha index, mean depth was the best predictor, with mean conductivity also important (total r^2 = 0.41). Both evenness indices had only one significant predictor, stone associ-

Table 5.4. Results of a stepwise regression analysis of pooled seasonal measures of Margalef's index, the log series alpha index, the Berger-Parker dominance index and Simpson's index against 26 biological, physicochemical and stability measurements. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Parameter estimate	Partial r^2	Model r^2
MARGALEF'S INDEX			
Intercept	4.13		
Mean stone movement	-0.03	0.51	0.51
Mean conductivity	0.01	0.11	0.61
Tractive force	0.01	0.06	0.67
Stone associated POM	0.04	0.03	0.70
LOG SERIES ALPHA INDEX			
Intercept	7.63		
Mean depth	-0.16	0.29	0.29
Mean conductivity	0.03	0.12	0.41
BERGER-PARKER DOMINANCE INDEX			
Intercept	2.51		
Stone associated POM	0.11	0.18	0.18
SIMPSON'S INDEX			
Intercept	4.42		
Stone associated POM	0.25	0.22	0.22

ated POM which accounted for 18% and 22% of the variation in the data for the Berger-Parker index and Simpson's index, respectively.

The influence of stability on seasonal variation (i.e., the coefficient of variation for the five seasonal samples) also differed between the two index groups. For both Margalef's index and the log series alpha index, variation increased with a decrease in the overall stability of a site (Fig. 5.9) ($F = 8.68$, $df = 1,9$, $P < 0.05$, $r^2 = 0.49$, and $F = 4.63$, $df = 1,9$, $P < 0.05$, $r^2 = 0.34$ for Margalef's and the log series alpha indices, respectively) Seasonal variability in the two evenness indices were not related to the stability of the site, however (Fig. 5.9) ($F = 0.004$, $df = 1,9$, $P > 0.05$, $r^2 = 0.00$, and $F = 1.21$, $df = 1,9$, $P > 0.05$, $r^2 = 0.12$ for the Berger-Parker index and Simpson's index, respectively).

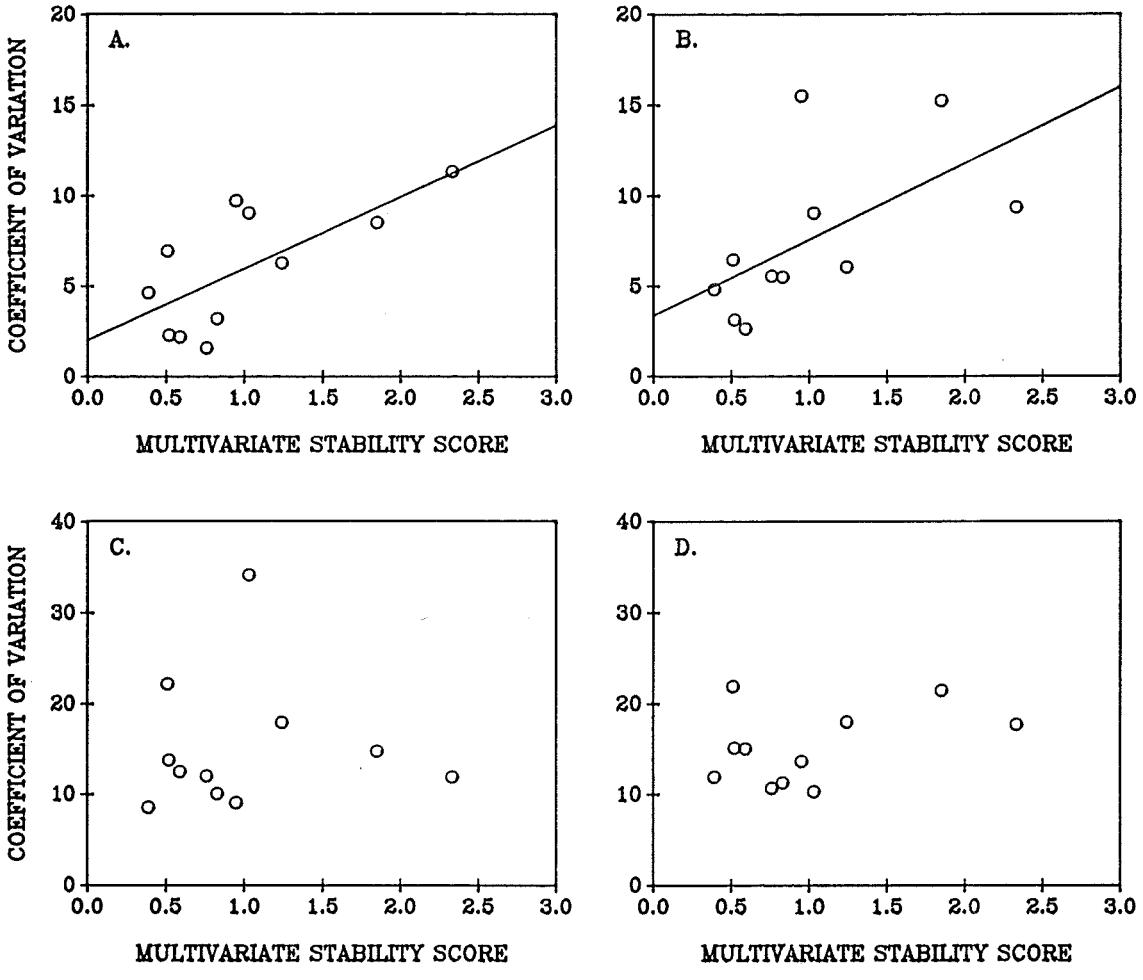


Figure 5.9. Coefficient of variation of Margalef's index (A), log series alpha index (B), Berger-Parker dominance index (C) and Simpson's index (D) over the five seasons as a function of overall stability. Regression analyses for the Berger-Parker dominance index and Simpson's index were nonsignificant (r^2 = 0.001 and r^2 = 0.12, respectively), but those for Margalef's index and the log series alpha index yielded the equations: seasonal CV = 2.01 + 3.97(stability score), r^2 = 0.49 and, seasonal CV = 3.35 + 4.22(stability score), r^2 = 0.34, respectively.

DISCUSSION

In the present study, species number declined as overall stream stability decreased, and of the 26 environmental variables examined, stability was the single best predictor of the number of species at a site. This is consistent with the results of Robinson & Minshall (1986) who found a decrease in species number on artificial substrates with increasing frequency of disturbance. Boulton *et al.* (1988) also found that more severely disturbed substrates (acid scoured stones as opposed to brushed ones) took longer to regain pre-disturbance diversity levels. It is also consistent with the results of several studies of marine communities in which the greatest diversity occurred at the lowest level of disturbance (Lubchenco, 1978; Lubchenco & Gaines, 1981). In other experimental manipulations (Clifford,

1982; Doeg *et al.*, 1989) and studies of flood events (Siegfried & Knight, 1977; Fisher *et al.*, 1982; McElravy *et al.*, 1989; Sagar, 1986; Scrimgeour & Winterbourn, 1989) disturbances have also been found to lower species number, and it is plausible that frequent disturbances (at least those above a particular threshold) will lead to the maintenance of low species diversity.

Lake *et al.* (1989), however, found that similar numbers of species recolonised disturbed patches whether they had been disturbed once or three times prior to monitoring community recovery. Although, it seems to me that time since the last disturbance will have a greater influence on species diversity than the number of disturbances a patch experiences *per se*. A rather confusing point as to whether increased disturbance frequency affects community composition by decreasing the time since the last disturbance (and therefore the time for recovery; as in the study by Robinson & Minshall (1986)), or whether it is the number of disturbances a patch experiences that affects community composition, independently of the time for recovery (as in Lake *et al.*, 1989). Reice (1984, 1985) also found no impact of disturbance frequency or disturbance *per se* on species number or "diversity" (i.e., H′) in experimentally disturbed baskets of substrate, and concluded that all taxa were affected equally by the disturbance.

It should be noted that most of the above mentioned studies either address the effects of disturbance frequency (e.g., Robinson & Minshall, 1986) or disturbance intensity (e.g., Boulton *et al.*, 1989). In contrast, environmental stability was assessed in my study by changes in the environment not the frequency or intensity of disturbance events. For example, a large amount of substrate movement in any one month could have resulted from a single large disturbance, or from several smaller, but more frequent disturbances. Whether increases in frequency or intensity of disturbance have similar effects on stream biotas and how they may interact (e.g., with respect to the area affected by a disturbance) awaits investigation.

The strong linear relationship I found between species number and disturbance intensity is not consistent with the intermediate disturbance hypothesis unless my most stable sites are considered to represent intermediate levels of disturbance in a broader perspective. I consider this unlikely however, as few running water habitats would be more stable than the upper reach of a spring-fed stream. Petraitis *et al.* (1989) in their theoretical review of diversity models suggested that the nature of the relationship between disturbance and diversity would depend on the balance between immigration and extinction rates as patch recolonisation proceeded following a disturbance. The scenario of the intermediate disturbance hypothesis only eventuates if the extinction rate exceeds the

immigration rate as colonisation proceeds. If extinction and immigration rates form a dynamic equilibrium, or if both decrease to zero, then more stable patches will have greater diversity. What factors control immigration and extinction rates in stream habitats and how they interact to generate diversity patterns is an essentially unanswered question in stream ecology (but see Sheldon, 1984).

Support for Huston's (1979) dynamic equilibrium model in my data is difficult to assess without any knowledge of whether competitive displacement could be occurring in any of the streams or whether the rate at which it is occurring differs among sites. I found a strong positive relationship between stability and periphyton biomass (and conceivably primary production), but whether competition among invertebrates is affected by changes in productivity is unclear. More limiting resource levels may increase the effects of competition between invertebrates, or alternatively high resource levels may provide disproportionately more resources for superior competitors and in this way enhance competitive exclusion (McGuinness, 1987). My data provide no suggestion that competitive exclusion was occurring, if it is assumed that immigration rates did not increase with time since disturbance, or if it was occurring then it was proceeding too slowly to reach completion, even at the most stable sites.

The nature of the relationship between stability and species number remained remarkably constant over all seasons, despite the stability of some sites decreasing during winter and spring 2. This seemed to be because both stable and highly unstable sites maintained proportionally similar numbers of species. Whereas sites of intermediate stability exhibited a greater decrease in species number in the more unstable seasons. The fact that the biota of the most unstable streams did not appear to be affected by increased disturbances is rather surprising, as many of the disturbances were severe, and stream channels moved 20 m or more laterally in some flood events. It therefore suggests that the fauna is not only highly resilient (i.e., able to recolonise effectively following a disturbance) but also fairly resistant (i.e., able to survive during a disturbance) to conditions, perceived as harsh (some streams were in flood at the time of collection). Several authors have provided evidence of the ability of stream faunas to cope with disturbances (e.g., Gray, 1981a; Reice, 1985; Sagar, 1986; Scrimgeour & Winterbourn, 1989), but whether this is via resilience or resistance to flood events probably depends on the particular species involved.

Total numbers of individuals showed a similar decline to species number with decreasing stability, however the closest correlations were with periphyton biomass at a site. This suggests that primary productivity of the stream bed, may be more important than stability in dictating the overall carrying capacity for inverte-

brate communities, although productivity is also closely linked with stability (see Chapter 3). All of the above mentioned studies (see references cited above in relation to the diversity/disturbance debate) have shown reductions in invertebrate densities with disturbances. Similarly, the two diversity measures of species richness showed a somewhat weaker linear decline in diversity with a decrease in stability.

Species evenness or dominance, however, showed no linear relationship with stability, and evenness peaked at the sites of intermediate stability with the same level of dominance in both very stable and unstable sites. This suggests that Huston's (1979) dynamic equilibrium hypothesis may have some applicability in this situation. Competitive displacement may have been occurring at the very stable sites, but so slowly that exclusion of all individuals of a species does not reach completion. Alternatively, given the very patchy nature of stream environments it may be that a particular species can be removed from many patches by competitive exclusion, but is able to survive in others, either because conditions ameliorate such competitive effects or simply by continual movement. Thus, although some successful competitors may become dominant in very stable environments they do not completely eliminate inferior species. A mathematical treatment of this idea has shown complete competitive exclusion can be prevented by habitat patchiness (Kishimoto, 1988, 1990). Consequently when viewed at the level of the patch, the dynamic equilibrium model may be applicable but it need not be when viewed at the level of the stream reach.

In summary, it is apparent that a strong relationship exists between environmental stability and diversity (both species richness and species evenness), however the mechanism of its maintenance is difficult to assess. Stability may not only affect diversity directly but may also act through its interaction with other factors, e.g., habitat heterogeneity, productivity (periphyton biomass), or even periphyton diversity. Similarly the overall density of invertebrates at these sites is also intimately linked with stability and/or its effects on productivity.

CHAPTER 6

SPECIES-ABUNDANCE DISTRIBUTIONS

INTRODUCTION

Diversity can be a misleading concept because of the difficulty of assigning a single measure to a multidimensional parameter. The previous chapter is a good illustration of this difficulty, with differing effects of environmental stability on the two components of diversity, i.e., species richness and species evenness. Consequently, some workers (e.g., May, 1975, 1981; Southwood, 1978) have strongly advocated the use of the entire species-abundance distribution as providing the only sound basis for examining species diversity.

The species in any given community will not all be equally represented; there will be some that are very common, some of intermediate abundance and the remainder represented by only a few individuals. The relationship between species number and the abundance of these species within the community is known as the species-abundance distribution. A number of models have been developed to describe observed patterns in these distributions. Some of them have their theoretical base in ecology, whereas others are fundamentally statistical models (Gray, 1987), and although the ecological mechanisms that generate these distributions are not always clear (Gray, 1987) they may be useful descriptors of a community in their own right (e.g., Gray *et al.*, 1985).

Models that have been applied to species-abundance distributions have been reviewed by Pielou (1975), May (1975), Engen (1978), Frontier (1985) and Magurran (1988). The four most common are the geometric series (Motomura, 1932), the broken-stick model (MacArthur, 1957), the log series distribution (Fisher *et al.*, 1943) and the log normal distribution (Preston, 1948). Other models that have also been applied are the Zipf-Mandelbrot model (Zipf, 1949; Mandelbrot, 1977) and the negative binomial (and gamma) distribution (Arrhenius, 1922; Gleason, 1922). However, they have been less widely used and will not be considered here. Tokeshi (1990) has recently applied a number of models based on random niche apportionment to epiphytic chironomid communities.

The four principal models can be considered to represent a progression in community composition; ranging from the geometric series where a few species dominate and the remainder are fairly uncommon, through the log series and log normal distributions where species of intermediate abundance become more common, and finally to the broken stick model where species distribution is most

equitable (Magurran, 1988). Each of the models has a characteristic shape on a rank/abundance plot (Fig. 6.1) (Whittaker, 1977). If the abundance of a species in some way reflects the portion of niche space it occupies, then the models may also be considered to represent a gradient with one or a few species monopolizing a large proportion of the niche hyperspace at one end (geometric series), and resources being more evenly divided (broken stick model) at the other (Southwood, 1978).

The Geometric Series

In this model the dominant species pre-empts proportion k of some limiting resource, the second most dominant pre-empts the same proportion k of the re-

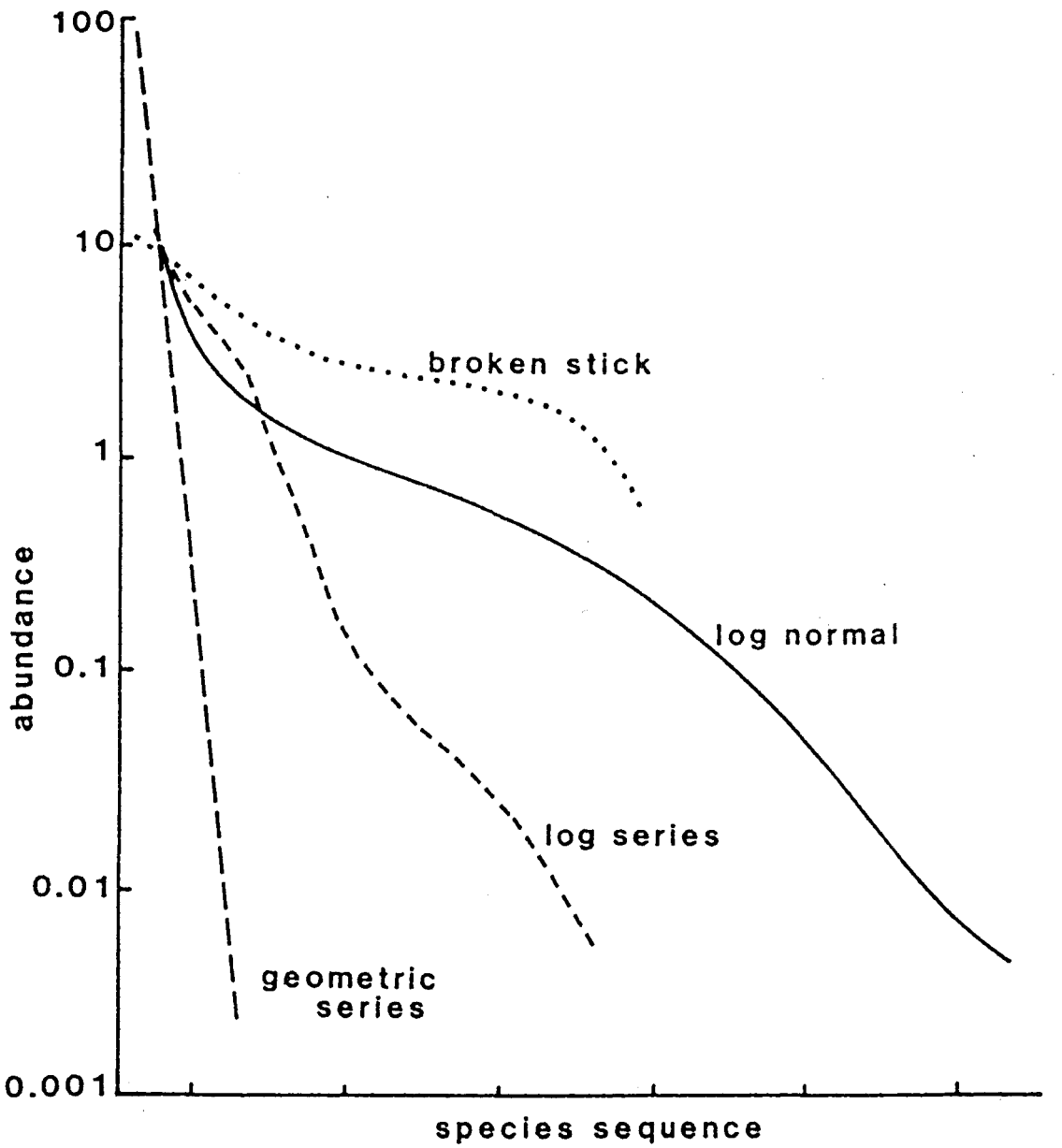


Figure 6.1. Hypothetical rank abundance plots for the geometric series, log series, log normal and broken stick models showing their typical shapes.

mainder, the third species taking k of what is left and so on, until all species have been accommodated. This scenario often fits the situation where a single environmental resource is extremely important to species survival, and is utilized in a strongly hierarchical manner. If the abundances of species are proportional to the amount of resource that they utilize, then a geometric series (also known as the niche pre-emption model) of species abundances will result. The abundance of species ranked from most to least abundant is given by:

$$n_i = NC_k(1-k)^{i-1}$$ (May, 1975; Motomura, 1932)

where n_i = the number of individuals in the ith species;

N = the total number of individuals;

$C_k = [1-(1-k)^S]^{-1}$ and

S = the total number of species.

The geometric series fits communities poor in species, such as those in early stages of succession (Whittaker, 1975), or those in extremely polluted environments (Gray, 1981b) where dominance of one or a few species is high. As succession proceeds, or conditions ameliorate, the species-abundance pattern will tend to grade into those of the log series distribution (e.g., Bazzaz, 1975) (Magurran, 1988).

The Log Series Distribution

This model was developed by Fisher (Fisher *et al.*, 1943) as a statistical distribution describing the relationship between the number of species and the number of individuals associated with those species. Mathematically, it is closely related to the geometric series (May, 1975). If species arrive at an unsaturated habitat at regular time intervals and occupy fractions of the remaining niche hyperspace, a geometric series will be predicted to occur. On the other hand, if the intervals of arrival between species is random rather than regular, a log series distribution should result (Boswell & Patil, 1971; May, 1975).

The log series distribution takes the form:

$$s_n = \frac{\alpha x^n}{n}$$

where s_n = the number of species predicted to have n individuals (Fisher *et al.*, 1943; Poole, 1974).

The total number of species (S) can be obtained by summing these terms for all classes to yield the equation:

$$S = \alpha[-\ln(1-x)]$$

x is estimated from the iterative solution of

$$S/N = (1-x)/x[-\ln(1-x)]$$

where N = the total number of individuals.

The small number of dominant species and the large proportion of rare species predicted by this distribution, like the geometric series, suggests that it will be most applicable to communities in which one or a few environmental factors dominate. It has been found to fit a wide range of ecological data (see Williams (1964) for a summary).

The Log Normal Distribution

Most species-abundance patterns that have been investigated fit the log normal distribution (Sugihara, 1980). It was originally proposed by Preston (1948) who observed that the number of species represented by a single individual was not the most abundant frequency class in many data sets. He proposed a model where the number of individuals per species, when plotted on a geometric scale (he used $\log_2$) against the number of species would follow a normal distribution truncated to the left of the mode. The truncation point represented rare species that were present in the community but not collected during sampling.

The distribution usually takes the form:

$$S(R) = S_0 \exp(-a^2R^2) \text{ (May, 1975)}$$

where S(R) = the number of species in the Rth octave (i.e., class) to the right and left of the symmetrical curve;

S_0 = the number of species in the modal octave and

$a = (2\sigma^2)^{1/2}$ = the inverse width of the distribution.

Although this model appears to fit a large number of data sets, the ecological reason(s) for this is not clear, and at least four hypotheses have been put forward to explain it.

The most common explanation is that the log normal distribution is the result of a wide range of environmental factors acting randomly on the community. According to the central limit theorem, the product of the effects of such a large number of random factors acting on individuals and species will be the log normal distribution (May, 1975).

Pielou (1975) proposed a sequential breakage model to explain the log normal distribution. She envisaged the resource axis of a community being randomly and sequentially split, the result of a large number of such splits being a log normal distribution. Sugihara (1980) invoked a similar explanation to explain the canonical log normal distribution, although in his model multidimensional niche space was sequentially apportioned, whereas Pielou considered only a single resource.

Another explanation is that the log normal distribution results from the mixing

of a large number of species whose populations are each growing logarithmically (May, 1975), and one of the most recent hypothesis is that the log normal distribution results from the summation of three underlying symmetrical distributions (Ugland & Gray, 1982). These are produced by groups of rare species (representing ~65% of the total), species with intermediate abundance (~25%) and very common species (~10%).

The Broken Stick Model

The broken stick model proposed by MacArthur (1957), has the most equitable distribution amongst the constituent species of a community, and represents a situation where an environmental resource is divided more or less evenly amongst the species. MacArthur likened the subdivision of a community's resource axis to a stick that is broken randomly and simultaneously into S pieces (whereas in Pielou's model of the log normal distribution, the breakages are sequential).

The number of individuals in the ith most abundant of S species (N_i) is given by:

$$N_i = N/S \sum_{n=i}^{S} 1/n \text{ (May, 1975)}$$

where N = the total number of individuals and
S = the total number of species.

A few studies, principally those dealing with narrowly defined taxonomic groups, have demonstrated a fit to the broken stick model (e.g., some passerine birds (MacArthur, 1960), minnows and gastropods (King, 1964)).

Strictly speaking, the model predicts the expected abundance of the ith species in a community and not the actual abundance of that species (Pielou, 1975); a census of a single community can therefore never provide evidence for or against the model. It predicts the average species-abundance distribution over a number of communities (Pielou, 1975). The model is also unclear about whether resources are divided amongst species as a result of evolutionary adaptation to a particular resource range, or as a consequence of local competitive interactions (Gray, 1987) Many workers have therefore abandoned it as unrealistic (Gray, 1987). However, a fit to the broken stick model still indicates that the species-abundance distribution is more even than it is if any of the other three distributions are the best fit.

Species-Abundance Distribution Models and Environmental Stability

A considerable amount of evidence suggests that communities at an early stage of succession fit the geometric series, but that as succession proceeds they will de-

velop through the log series and log normal distributions and eventually may return to a geometric series at their climax (Whittaker, 1975). If disturbance can be seen as resetting the successional stage of a community it can be hypothesized that a similar pattern should emerge in communities occupying increasingly stable environments.

However, some controversy has arisen recently over the ecological interpretation of data that fit the log normal and log series distributions (Gray, 1987). May (1981) suggested that "equilibrium" communities often fit the log normal distribution, and that when a community is disturbed the species distribution pattern reverts to the less equitable log series distribution. For example, this appeared to have been the case for stream diatom communities subjected to organic pollution (Patrick, 1973). Shaw *et al.* (1983), Kempton & Taylor (1974), Lambshead & Platt (1985) and Hughes (1985) have argued however, that the log series distribution fits data from undisturbed communities, and that the log normal fits communities from disturbed habitats. Yet May (1975) has also maintained that any large assemblage of species influenced by a variety of random factors would follow the log normal distribution.

An ecological interpretation of the log series distribution is similarly problematic. Thus, Stenseth (1979) suggested it should fit unstable communities (i.e., those where population densities fluctuated), and Caswell (1976) considered it should apply to communities where biological interactions were not important. These ideas need not be mutually exclusive, and Gray (1987) contended that ecological interpretations could not be assessed because of a lack of definition of terms (e.g., "equilibrium" and "disturbance") employed in different studies.

A number of studies of stream invertebrate communities have attempted to fit one or more of these species-abundance distributions to observed communities. Townsend *et al.* (1983) found that the rank/abundance distributions of 34 stream invertebrate communities exhibited a range of curves from the geometric series through to the broken stick distribution. These patterns did not appear to correspond to any of the environmental variables they measured, although one group of seven low pH stations did exhibit a consistent pattern of low equitability and high niche pre-emption constants.

Shepard (1984) found that all the invertebrate communities at sites along eight Idaho streams were adequately described by the log series distribution. Bruns & Minshall (1983) found that the predaceous invertebrate communities of the Salmon River, Idaho did not fit the log normal distribution, whereas Minshall *et al.* (1985) found that communities at four sites on that river conformed more closely to the log normal distribution in summer than in autumn. They took this to indicate a swing from communities at "relative equilibrium" in summer, to ones at "relative nonequilibrium" in winter.

Most recently, Tokeshi (1990) contrasted five niche apportionment models (i.e., geometric series, dominance preemption, random fraction, MacArthur fraction and dominance decay) with two lacking conventional niche apportionment (i.e., random assortment and a combined niche apportionment and random assortment model) as descriptors of epiphytic chironomid communities. He found the random fraction and random assortment models fitted distributions based on numbers of individuals, whereas only the random assortment model fitted biomass data. Tokeshi concluded that these communities represented a dynamic system not structured by niche apportionment.

Only two of the above studies appear to have addressed the question of whether or not the underlying species-abundance model which best describes a community is related to the streams physicochemical environment. The aim of the work discussed in this chapter was therefore to examine the influence of environmental stability on the species-abundance distribution at each of my study sites and whether or not the model which best describes that distribution was also related to stability. I predicted that the unstable sites would have less equitable species-abundance distributions, strongly dominated by one or two species, and that they would be modelled best by the geometric or log series. In contrast, the stable sites were predicted to have more even species distributions and would be modelled best by the log normal distribution, or perhaps even the broken stick model.

MATERIALS AND METHODS

Models were fitted to mean density data sets (Appendix I) grouped into $\log_2$ classes, rather than the collected stone sample data sets (see Chapter 4). This was done to avoid modelling the sampling distribution rather than the underlying species-abundance distribution. Theoretical distributions were fitted to each data set using a Turbo BASIC program that I wrote (Appendix II). Estimates of x (from the log series distribution) and k (from the geometric series) were solved iteratively to an accuracy of six decimal places. A truncated log normal with the truncation point at 0.5, was fitted rather than a classical log normal. This was done to allow for rare species that are present in the community, but that are not collected in sampling because of their rarity (see Pielou, 1975). For all but the geometric series, model fit was assessed by comparing the expected class frequencies for each model with the observed frequencies using a chi-square test and the appropriate degrees of freedom. To test the geometric series fit, the number of individuals predicted for each species was compared with the observed number, again with a chi-square test.

RESULTS

The fit of the models to each of the data sets is given in Table 6.1. Only two of the data sets were not fitted by one of the four tested models, and the majority (53 out of 66) were fitted by at least two of the models at the 5% level. Models that fitted were predominantly the log series and the log normal distributions. All four models gave significant fits to three of the data sets, a situation that is not unusual

Table 6.1. Probability values for comparisons of observed species-abundance distributions with four common species-abundance models as indicated by chi-square tests of goodness of fit. Sites are listed in order from least stable to most stable as measured by their multivariate stability scores (Chapter 2). Given probabilities are those for rejection of the null hypothesis (i.e., that the two distributions are equal). Therefore when two models fit the same data set, the model with the higher probability would be more likely to have produced the observed difference by chance alone and can be considered the best fit for the observed distribution (indicated by *). Model distributions were rejected if the probability of getting the observed difference by chance alone was less than 5% (indicated by -).

Site		Geometric Series	Log Series	Log Normal	Broken Stick
BRUCE STREAM	Spring 1	-	0.3*	0.2	0.1
	Summer	-	0.95*	0.8	0.1
	Autumn	-	-	0.7*	-
	Winter	0.8*	0.3	0.5	0.5
	Spring 2	0.99*	0.2	0.2	0.1
	Pooled	-	0.3	0.7*	-
KOWAI RIVER	Spring 1	-	0.2	0.5*	-
	Summer	-	0.3*	-	-
	Autumn	-	0.2	0.7*	-
	Winter	-	-	0.2*	-
	Spring 2	-	0.2	0.3*	-
	Pooled	-	-	-	-
DRY STREAM	Spring 1	-	0.5*	0.3	-
	Summer	-	0.7*	0.1	-
	Autumn	-	0.8*	0.7	-
	Winter	-	0.5	0.9*	-
	Spring 2	-	0.7	0.9*	-
	Pooled	-	0.98*	0.7	-
WHITEWATER STREAM	Spring 1	-	0.9*	0.7	-
	Summer	-	0.7*	0.5	-
	Autumn	-	-	-	-
	Winter	-	0.7*	0.5	-
	Spring 2	-	0.5*	-	-
	Pooled	-	0.9*	0.8	-

Table 6.1. (*Continued on following page*)

Table 6.1. (*Continued*)

CRAIGIEBURN CUTTING STREAM	Spring 1	-	0.2*	0.28	-
	Summer	-	0.99*	0.9	-
	Autumn	-	0.95*	0.3	-
	Winter	-	0.5*	0.5*	-
	Spring 2	0.2	0.5	0.7*	0.2
	Pooled	-	0.8*	-	-
GRASMERE STREAM	Spring 1	-	0.2	0.3*	-
	Summer	-	0.2*	0.2*	-
	Autumn	-	0.98*	0.3	-
	Winter	-	0.9*	0.5	-
	Spring 2	-	0.5	0.7*	-
	Pooled	-	0.3	0.5*	-
MIDDLE BUSH STREAM	Spring 1	-	0.5	0.7*	-
	Summer	0.5	0.7*	0.5	-
	Autumn	-	0.5*	0.5*	-
	Winter	-	0.3	0.95*	0.2
	Spring 2	-	0.3	0.7*	0.7*
	Pooled	-	-	0.5*	-
PORTER RIVER	Spring 1	-	0.5	0.8*	-
	Summer	-	0.3	0.9*	-
	Autumn	-	0.7*	0.5	-
	Winter	-	0.3*	0.3*	-
	Spring 2	-	0.98*	0.5	-
	Pooled	-	0.7	0.8*	-
LAKE GRASMERE	Spring 1	-	-	0.1*	-
	Summer	-	-	0.1*	-
	Autumn	-	0.5	0.7*	-
	Winter	-	0.5	0.8*	-
	Spring 2	-	0.5	0.98*	-
	Pooled	-	-	0.7*	-
CORA LYNN STREAM	Spring 1	-	0.5*	0.3	-
	Summer	-	0.3	0.8*	-
	Autumn	-	0.2*	-	-
	Winter	-	0.8*	0.5	-
	Spring 2	-	-	0.2*	-
	Pooled	-	0.8*	0.1	-
SLIP SPRING	Spring 1	-	0.5*	0.2	-
	Summer	-	0.7*	0.1	-
	Autumn	-	0.3	0.7*	-
	Winter	-	0.7*	0.5	-
	Spring 2	-	0.7	0.9*	-
	Pooled	-	0.5*	0.1	-

for samples containing few species (Magurran, 1988) (all three sets had fewer than 15 species, the least of all the sets).

Although most of the observed species-abundance distributions were fitted by more than one model at the 5% level of significance, when considered over a spectrum of probabilities one of the models could in general be distinguished as being a better fit than the others. This was confirmed by visual inspection of a plot of the observed class frequencies and the associated expected frequencies for each model. Those for the pooled data sets (i.e., all seasons combined) at each site are shown in Fig. 6.2.

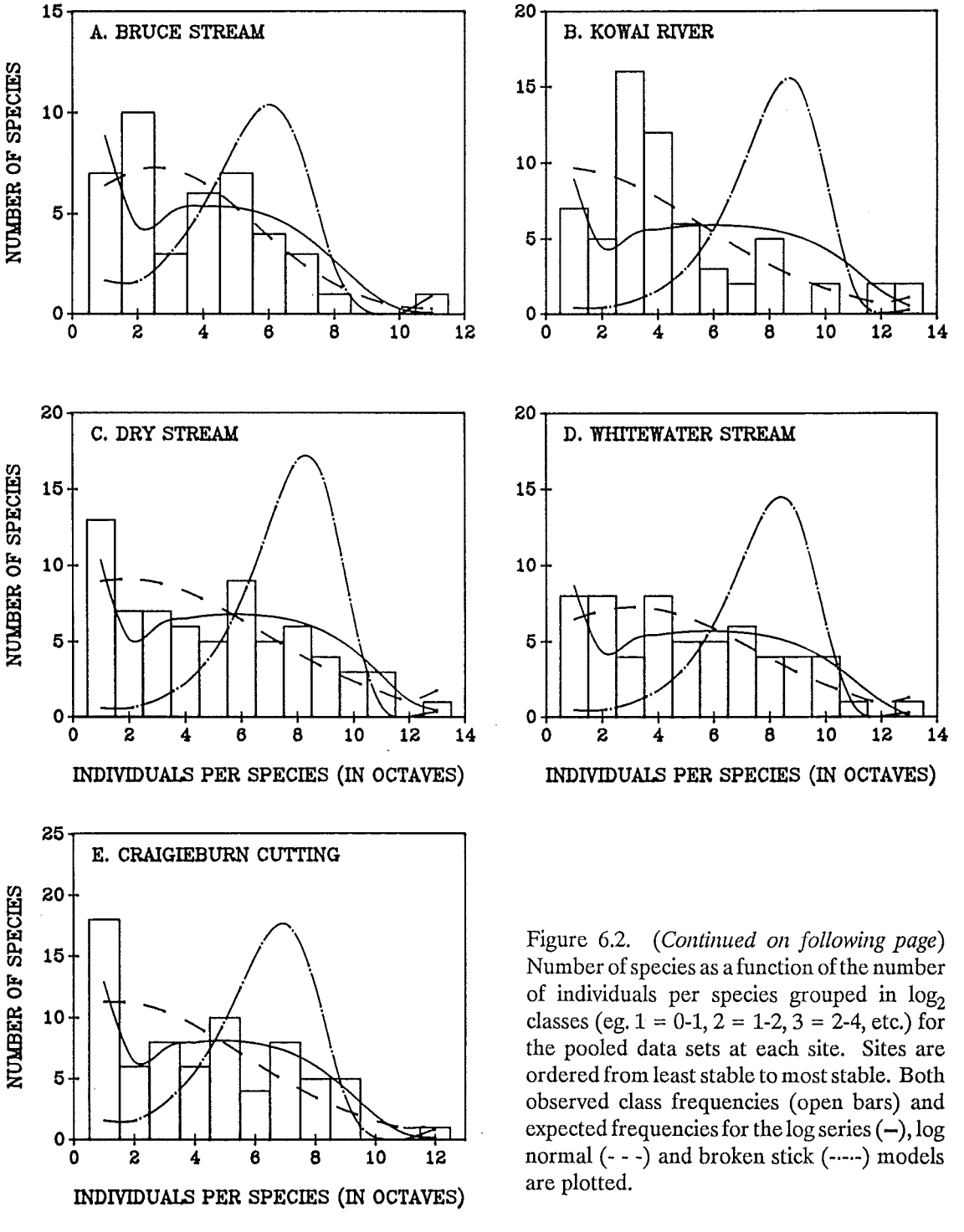
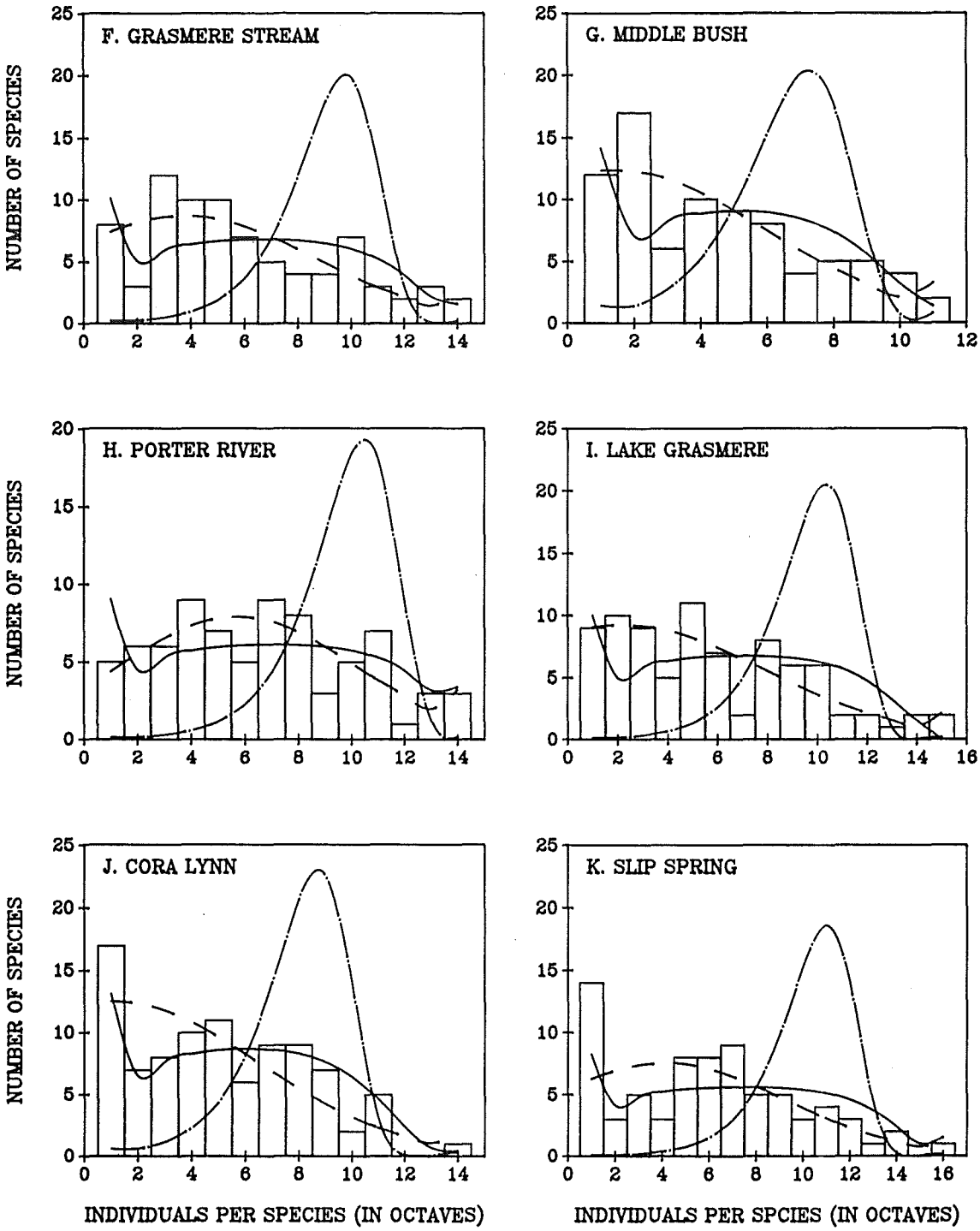


Figure 6.2. *(Continued on following page)* Number of species as a function of the number of individuals per species grouped in $\log_2$ classes (eg. 1 = 0-1, 2 = 1-2, 3 = 2-4, etc.) for the pooled data sets at each site. Sites are ordered from least stable to most stable. Both observed class frequencies (open bars) and expected frequencies for the log series (—), log normal (- - -) and broken stick (·····) models are plotted.

Figure 6.2. (*Continued*)



Only two site communities were modelled best by the same theoretical distribution in all seasons. The Lake Grasmere community was fitted best by the log normal distribution and the Whitewater Stream community was fitted best by the log series distribution. The other sites were fitted best by different models in different seasons.

DISCUSSION

At first glance my results appear to mirror the confusion that exists in the literature, with different models fitting the same site at different times. In the only other study of this type to include seasonal comparisons, Minshall *et al.* (1985) also found a shift from a close fit to the log normal distribution in summer, to a weaker fit in autumn. They suggested that this may represent a shift from equilibrium communities in summer to nonequilibrium communities in autumn; they did not however, test whether other models may have produced better fits in either season. During periods of stable flow, conditions are more likely to approach those necessary for "equilibrium" communities (or at least communities with more equitable distributions) to develop. It is probably not surprising therefore, that the form of the species-abundance distribution (as indicated by the model of best fit) changed as both the season and the stability of the sites changed. Bruce Stream for example, had a species-abundance distribution modelled best by the geometric series in winter and spring 2 (the seasons with the most unstable conditions), by the log series in spring 1 and summer and by the log normal in autumn (one of the most stable seasons).

However, what if seasonal effects (such as changes in stability) are removed; do the sites then have varying species-abundance distributions related to their overall stability? To throw some light on this it is possible to examine the frequency distributions for the pooled data sets (Fig. 6.2), in which seasonal effects should be evened out.

Of the unstable sites, three (Dry Stream, Whitewater Stream and Craigieburn Cutting Stream) were modelled best by the log series distribution. Log plots of their relative abundances (Fig. 6.3) indicate that communities at these sites were strongly dominated (at least numerically) by a single taxon (*Deleatidium*). They contained a large number of rare species, but only a moderate number of species in the intermediate abundance classes (Fig. 6.2).

Bruce Stream, the most unstable site, had the closest fit to the log normal distribution according to the chi-square statistic. Some caution needs to be shown when considering results of the goodness of fit tests for these models however, because of the small number of classes involved. Thus, differences between the models can be a consequence of the way species are allocated between two or three classes (Magurran, 1988). Some investigators (e.g., Lambshead & Platt, 1985; Hughes, 1986) have even rejected goodness of fit tests altogether in favour of graphical inspection. Although a combination of the two techniques seems most valuable for interpretation, and for Bruce Stream it appears that graphical

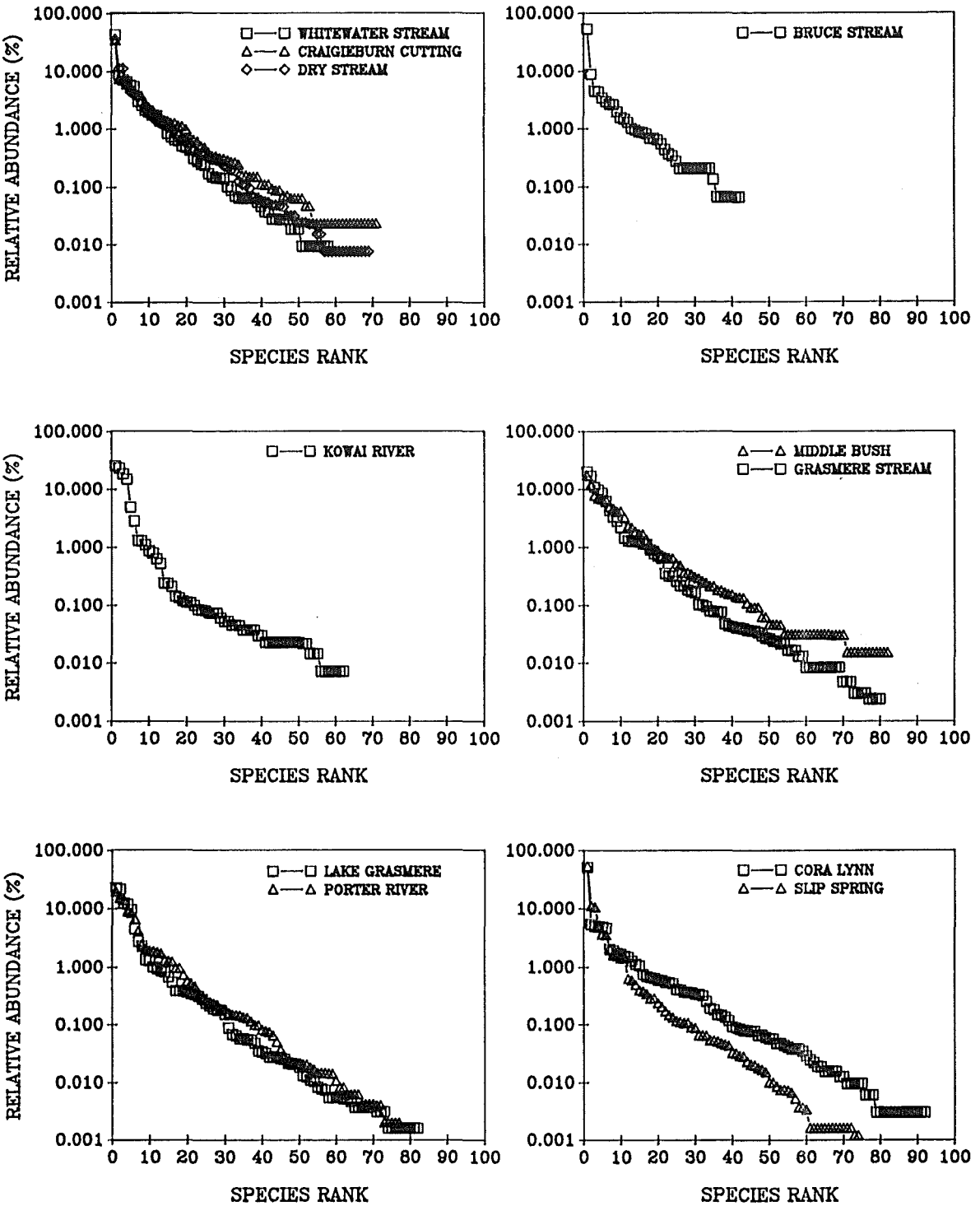


Figure 6.3. Mean relative abundance of the species collected at each site as a function of the rank of that species in the community. The most abundant species is on the left of the X-axis.

inspection is the most enlightening. An examination of the frequency distribution and the associated predicted frequencies for Bruce Stream (Fig. 6.2), reveals that the larger chi-square statistic for the log normal distribution was a result of a greater number of species in class two (1-2 individuals) than in class one (0-1 individuals), a phenomenon that is likely to have been strongly influenced by

chance events. A moderate number of intermediate species were present and one very dominant species (Fig. 6.3). The pattern obtained is more similar to the log series than the log normal distribution, however, because the rare species were split fairly evenly between the first two classes the chi-square goodness of fit test is unable to detect this. Thus the species-abundance distribution at Bruce Stream also appears to be modelled best by the log series distribution.

Kowai River had a species-abundance distribution that differed from that found at all other sites, and did not conform to any of the theoretical models. Most of its species were in abundance classes 3 (2-4 individuals) and 4 (4-8 individuals) (Fig. 6.2) with numerical dominance shared relatively evenly by four species (Fig. 6.3)

Four of the stable sites, Grasmere Stream, Middle Bush Stream, Porter River and Lake Grasmere were modelled best by the log normal distribution. Their frequency distributions (Fig. 6.2) were relatively uniform and similar numbers of species were found in the rare and intermediate abundance classes. Not surprisingly, their relative abundance plots were also fairly uniform and no one species predominated (Fig. 6.3). At the two most stable sites, Cora Lynn Stream and Slip Spring, the species-abundance distributions were again modelled best by the log series distribution. Both sites had a single very dominant species (Fig. 6.3) (*Potamopyrgus antipodarum* at Cora Lynn and *Maoridiamesa harrisi* at Slip Spring), and a large number of rare species.

It seems therefore, that with the exception of Kowai River, the unstable sites exhibited similar species-abundance distributions, with a single very dominant species and a large number of relatively rare species, and that they were modelled best by the log series distribution. Communities in streams of intermediate stability had more uniform distributions with no species strongly dominant, and were modelled best by the log normal distribution, whereas the most stable streams like the most unstable ones were modelled best by the log series distribution, and like them had a single dominant species and a large number of rare species.

This, not surprisingly, mirrors the response of the evenness diversity measures discussed in Chapter 5, the greatest evenness being recorded at the sites of intermediate stability. In that chapter I suggested that the high species number, but low evenness recorded at very stable sites may have been the result of competitive exclusion proceeding so slowly that it did not reach completion, or a consequence of inferior competitors being able to persist in refuge patches. Both these scenarios are contingent upon competitive dominance occurring in these stream communities, however, and although this has been demonstrated in a number of studies (e.g., McAuliffe, 1984a, 1984b; Hart 1985; Hawkins & Furnish, 1987; Hem-

phill, 1988; Dudley *et al.*, 1990) it is unclear whether competitive dominance occurs widely in streams (Reice, 1985). The dominance of *Maoridiamesa harrisi* and *Potamopyrgus antipodarum* may just as easily have been the result of high levels of oviposition or fecundity.

It must also be remembered that competitive hierarchies need not necessarily be expressed in terms of numerical dominance, but may equally well equate with differences in biomass (not considered here). Nevertheless, it is interesting to note that despite large differences between biomass and densities of species in epiphytic chironomid communities, Tokeshi (1990) found that data based on both criteria were approximated best by his random assortment model.

Irrespective of the underlying cause of the differences in the abundance of taxa it is still apparent that communities in unstable streams are modelled best by the log series, that those of intermediate stability are modelled best by the log normal distribution and those in very stable streams are again modelled best by the log series distribution. This also helps explain some of the large seasonal variation in model fits at each of the sites. Not only can communities shift from log series to log normal distributions as conditions become more stable but eventually they may revert to the log series distribution if conditions become even more stable.

This may help explain some of the conflicting statements in the literature. A log series distribution can describe an undisturbed community if one or two species are able to become dominant (for example, by competitive superiority), however, the log normal distribution is more likely to occur if none of the species can gain a strong numerical advantage. In contrast, the physically unfavourable nature of a disturbed environment for most species, usually appears to be advantageous to only a few species and the log series distribution results.

Therefore, if physical conditions at a site are such that any species is advantaged over others, either through competitive superiority or an ability to persist in the face of "harsh" physical conditions, a log series distribution will result. If, however, no species in the community are strongly advantaged over others, a log normal distribution should result. Furthermore, if conditions become extremely harsh the geometric series can be expected to be the best fit to the species-abundance distribution, as observed in Bruce Stream (the most unstable stream) following two major physical disturbances.

CHAPTER 7

COMMUNITY STRUCTURE

INTRODUCTION

In the two preceding chapters I dealt with the effect of environmental stability on macroscopic properties of community structure, but did not address questions relating to whether or not stability influences the particular suite of species that occurs at a site.

The influence of physicochemical factors on stream invertebrate communities has been a dominant theme of research in benthic ecology for many years (e.g., Macan, 1963; Hynes, 1970). With the advent of powerful multivariate statistical techniques (or more probably the development of computer packages to carry out such analyses) which are capable of searching for patterns in large data sets of both physicochemical and biological information, this line of research has shown no signs of abating. However, while the relationship between stream invertebrate community structure and associated physicochemical characteristics has received considerable attention (e.g., Townsend *et al.*, 1983; Bunn *et al.*, 1986; Moss *et al.*, 1987; Corkum, 1989 and references therein) the influence of stability or variability of the latter on invertebrate community structure has received comparatively little attention. Identification of any such relationships is difficult because most studies have been conducted over a wide range of streams, and any effects of environmental stability *per se* on community structure can not be readily separated from other influences of physical and chemical factors.

The effects of the physical and chemical environment on stream biota has also received considerable attention in studies of New Zealand stream communities. In fact Winterbourn *et al.* (1981) characterised New Zealand stream communities as being physically controlled, because of the overriding influence of New Zealand's physiogeography (i.e., relatively short rivers with high sediment yields (Griffiths, 1979)) and unpredictable climate. They contended that invertebrate communities in unmodified streams throughout New Zealand tended to have very similar faunas dominated by a widely distributed nucleus of thirteen genera and species. Rounick & Winterbourn (1982) provided some support for this contention, finding that the "core taxa" occurred at 43 forest streams throughout New Zealand despite large differences in the nature of their riparian vegetation.

Graesser (1988), in a survey of 23 South Westland streams also found the "common core" of taxa and concluded that a number of physicochemical factors

were important in structuring these invertebrate communities although no one parameter was of overriding importance. Chadderton (1990) in a study of 80 Stewart Island streams also found a common core of taxa, although the composition of the core on Stewart Island differed somewhat from that on the mainland, particularly in the absence or rarity of the Conoesucidae, Notonemouridae and Megaloptera, probably because of the island's isolation. Nevertheless, he concluded that differences in the relative abundance of these and other species in Stewart Island streams were primarily a consequence of the interaction between geography, the presence of moss cover and several chemical parameters.

In contrast to these studies, Winterbourn & Collier (1987) found that invertebrate community structure in 34 West Coast streams was not closely linked with measured physicochemical factors but was more strongly influenced by the geographic proximity of the streams. Although Collier *et al.* (1989) in a study of similar streams, but encompassing a more extreme range of chemical characteristics (produced as a result of catchment modification), found that both extreme acidity and water temperature did influence benthic community structure.

In a study of 88 moderate-small rivers, including many in modified catchments, Quinn & Hickey (1990a) found that the degree of catchment development (mediated through nutrient levels and periphyton biomass) was the single most important factor controlling invertebrate community structure. However, their analysis did not examine community structure at higher taxonomic levels, but was based on broad ordinal and/or functional feeding groups and this may have lead to some loss of discriminating power between their communities. Quinn & Hickey (1990b) also found that the structure of these communities was affected by flows greater than 20 x the median flow. Similarly, Jowett & Duncan (1990) found that invertebrate community structure of these same 88 rivers was weakly linked with flow variability, although this linkage was probably also a result of differences in the degree of modification of the streams.

From these studies it can be concluded that when streams of radically different character are considered (i.e., modified versus unmodified, or highly acid versus circumneutral streams) then the nature of the physicochemical environment (such as the degree of catchment development or streamwater pH) does influence invertebrate community structure. However, it also appears that in many New Zealand streams, encompassing a wide range of physical and chemical characteristics, a common core of taxa forms the basis of invertebrate communities. More subtle differences between communities seem to be related to their geographic proximity and therefore the availability of colonists, and/or a variety of physical and chemical parameters.

While many of the above studies have implicated environmental stability as an important factor in structuring invertebrate communities, none has been specifically designed to investigate the effect of stability on invertebrate community structure over a narrowly defined physicochemical range. In this chapter I consider the influence of environmental stability on invertebrate species composition at my eleven study sites. The streams all occur within close geographic proximity to each other and are relatively similar in terms of geomorphology, hydrology and water chemistry (see Chapter 2); they do however, differ in environmental stability.

MATERIALS AND METHODS

Data sets were analysed with multivariate ordination and classification techniques. Principal components analysis (using the PRINCOMP procedure of SAS (1985)) was used to identify gradients in community structure. Data were log transformed (ln (x+1)) for this analysis. What environmental, biological or stability characteristics these gradients correspond to was then assessed with stepwise regression and Pearson product moment correlation procedures of SAS (1985). Stepwise regression was carried out using the 26 biological, chemical, physical and stability measurements listed in Table 7.2. Spot measurements are those made at the time of collection or in the month prior to the collection of samples. The critical probability for addition and removal of variables to the model was set at 0.05. The same variables were used in the correlation analysis. Nonlinear ordinations commonly applied in stream ecology (e.g., DECORANA) were not deemed necessary because the underlying environmental gradients were relatively narrow (Noy-Meir & Whittaker, 1977) and because most sites had a number of species in common (Williamson, 1978). Although some analysis revealed a slight arching effect (see Fig. 7.2), detrending this arch would not have improved interpretation of the underlying gradient.

Classification of site communities into distinct groups was carried out with cluster analysis (using the SAS CLUSTER procedure (SAS, 1985)). I used an average linkage clustering algorithm, and four distance measures to assess differences in several components of these communities. For some distance measures this involved constructing a similarity matrix (using a Turbo BASIC program which I wrote) for input directly into the SAS CLUSTER procedure. The distance measures were Euclidean distance (this examines differences in absolute densities); relative Euclidean distance (which examines differences in relative abundance); the Bray-Curtis dissimilarity index, a measure which emphasises the

proportions of species (and/or their density) shared between communities, and is deemed by many the most appropriate for ecological data (e.g., Beals, 1984; Ludwig & Reynolds, 1988), and finally the Euclidean distance of presence/absence data. The quantitative distance measures were calculated on log transformed data (ln (x+1)).

Both types of analyses were carried out on each of the seasonal samples separately, all seasons combined and the average for the five seasons.

RESULTS

The mean relative abundance of the five most abundant species at each site is shown in Table 7.1. The most notable feature of this table is that most of the species present in the top five at any given site were also found at many of the other sites, although not always in the top five. In fact, of the 185 species recorded, only 56 (30 %) occurred at only one site, and most of these (17) were at Lake Grasmere. It is apparent therefore that many of the species collected at these sites can occur over the range of physicochemical characteristics recorded in these streams, although the relative and absolute abundances of these species differed between sites.

Table 7.1. Mean relative abundance of the five most abundant species at each of the study sites. * indicates that the species was one of the ten most abundant species at that site and + indicates a species was present at that site.

TAXA	UNSTABLE					STABLE					
	Kowai River	Whitewater Stream	Dry Stream	Craigieburn Cutting Stream	Bruce Stream	Porter River	Slip Spring	Cora Lynn Stream	Middle Bush Stream	Grasmere Stream	Lake Grasmere
Neppia montana	+	+	+	10.34		*	*	*	7.07	+	+
Nematoda	+	+	+	+	3.73	+	+	+	*	+	*
Potamopyrgus antipodarum		+	+			+	11.69	41.31	+	+	10.28
Slavina sp.	*	*	*	4.82	*	*	*	*	*	+	26.06
Eiseniella sp.	+	+	+	+	*	+	+	+	6.88	*	+
Chydoridae sp.	+	+			+	+	+	+	+	+	21.34
Ostracoda sp. A	+	+		+		+	+	+	15.50	+	+
Harpactacoid Copepoda	+	+	+	*	+	10.97	3.51	+	+	+	*
Deleatidium sp.	28.58	42.85	39.01	36.56	47.86	11.63	*	7.78	9.88	*	+
Zelandoperla decorata	+	+	+	+	5.18	+		+		+	
Zelandobius furcillatus	*	+	+	+	4.09	+	+	+	+		+
Spaniocerca zelandica				4.09				+	*		
Austrosimulium alveolatum	10.72	*	*	*	*				+	*	+
Maoridiamesa harris	6.42	11.91	4.88	+	+	16.92	52.45	4.45	+	21.75	+
Paucispinigera sp.	+		+	*	*	+	+	+	9.41	+	+
?Rheocricotopus sp.	6.17	4.82	8.77	5.18	5.39	12.60	9.65	4.75	*	7.68	+
Eukiefferiella claripennis	21.27	6.24	10.36	+	+	8.14	5.21	*	+	7.84	+
Eukiefferiella sp. B	+						+		+	+	12.28
Cricotopus auklandensis	+	*	+	+	+	+	+	+	+	7.88	+
Aoteapsyche colonica	+	+	+	+			+		+	8.45	
Pycnocentrodes sp.	+	+	*	+	+	*	+	7.26	+	+	
Pycnocentrodes aureola											6.94
Beraeoptera roria	+	+	4.96			*	+	+		+	
Notoaturinae sp. A	*	5.13	+	+	+	+	+	+	*	+	+

Initial ordination of the sites, both for each season separately and for all seasons combined, separated the Lake Grasmere community from the other sites. Therefore, although it shared many taxa (65) with the other sites, its unique environmental conditions (a wave-washed lake shore) were sufficient to produce a distinctive community of invertebrates.

To examine differences between the stream invertebrate communities the ordination was repeated with the Lake Grasmere community excluded. The first two axes of this ordination, carried out on the annual average for each site, accounted for 23.2% and 17.6% of the variation respectively, and divided the sites into three broadly overlapping groups (Fig. 7.1). These were the unstable sites, forest sites and open, stable streams. Cora Lynn Stream (the dark triangle) was somewhat intermediate between the open stable sites and the forest streams, and although an open stable site, it passed through thick matagouri scrub immediately above the study site and consequently shared a number of taxa with forest sites.

Ordination of all the seasonal samples yielded the same general pattern (Fig. 7.2), although the first two axes accounted for only 13.4% and 9.2% of the overall variation. The seasonal samples from the various sites appeared in general to be

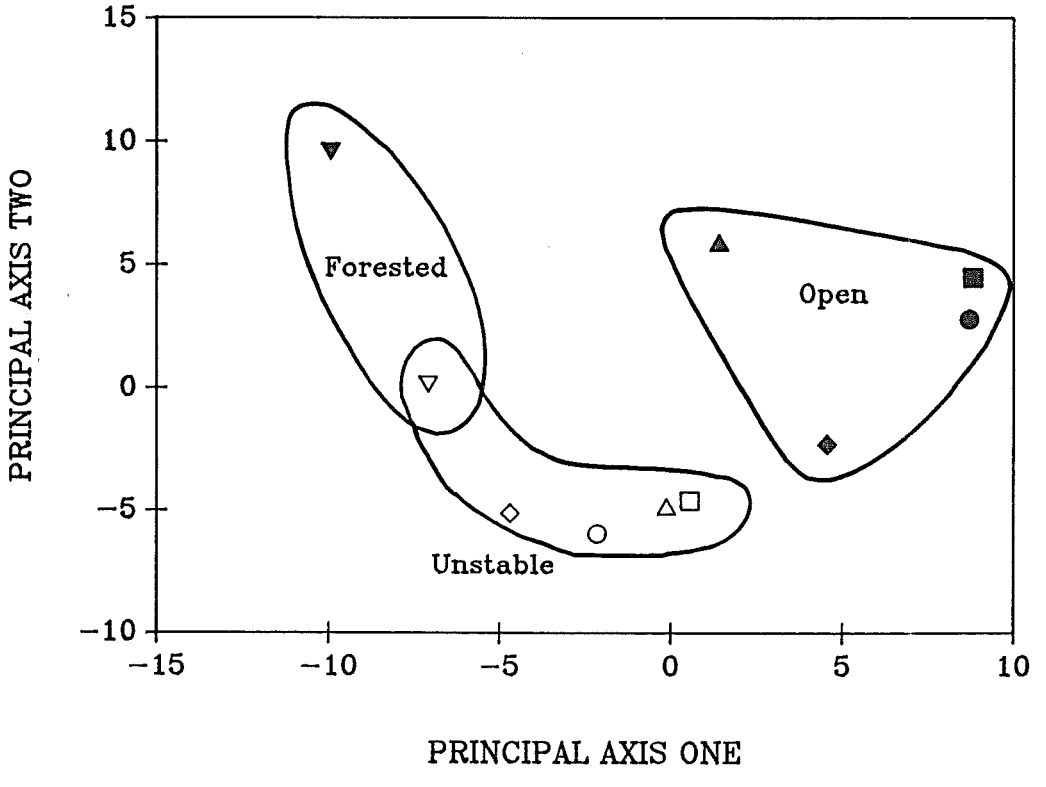


Figure 7.1. Principal axis two as a function of principal axis one for invertebrate communities of the ten streams; data from all five seasons are averaged. Site symbols are Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽), Bruce Stream (◇), Porter River (●), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆) and Slip Spring (■). Stable sites have filled symbols while unstable sites have open symbols.

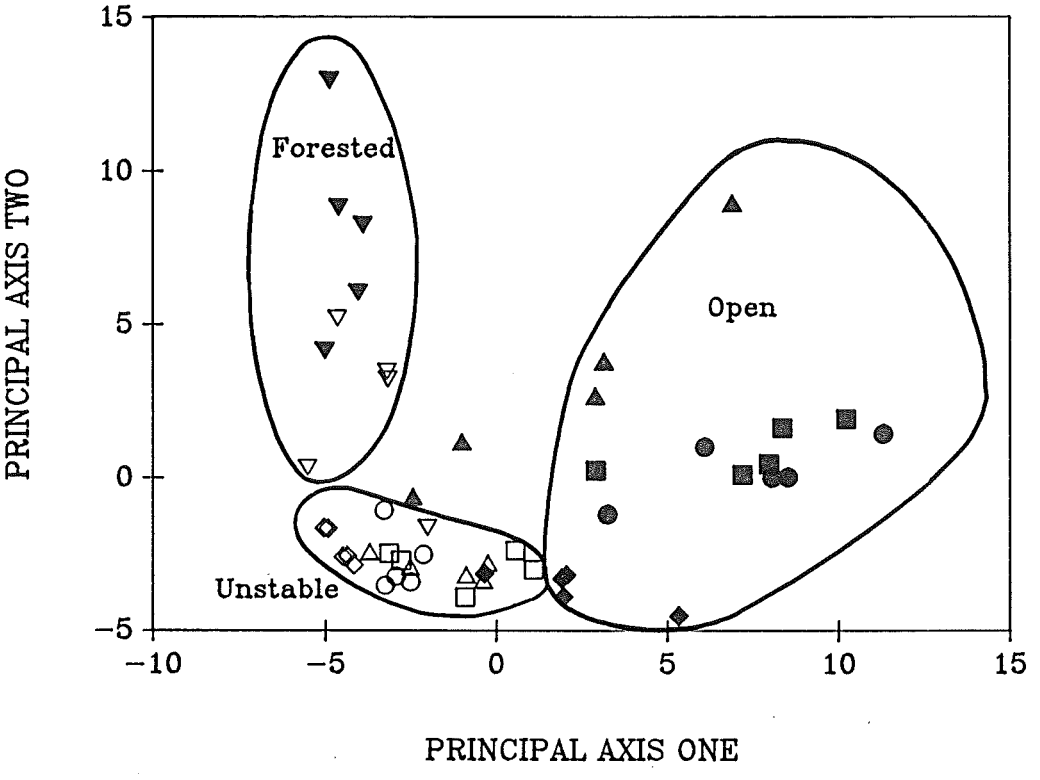


Figure 7.2. Principal axis two as a function of principal axis one for invertebrate communities of the ten streams in five seasons. Three broad groups are apparent: open stable sites, unstable sites and forest sites. Symbols as for Fig. 7.1.

more similar to themselves than to any of the other sites. Therefore, although a number of environmental characteristics (such as stability) changed seasonally at a site, the specific complex of environmental variables that exists at each particular site, must in itself be an important factor dictating community structure. Examination of differences between sites revealed that the unstable sites were more tightly grouped (i.e., more similar to each other) than were the stable sites, which suggests that their instability may constrain the degree to which the unique characteristics of a particular site can be expressed in its invertebrate community.

Axis one was negatively correlated with a number of stability measurements (Table 7.2) and positively correlated with epilithic pigment and organic carbon concentrations (although these variables are also correlated with stability, see Chapter 3). In a stepwise multiple regression (Table 7.3) the bottom component of the Pfankuch stability score came out as the single best predictor of the axis score (r^2 = 0.62), although a number of other variables were also important. The axis appears therefore to be related to stability, either directly or mediated through periphyton and organic carbon biomass. Axis two was negatively correlated with a large number of physicochemical and stability parameters (Table 7.2), although in a stepwise regression analysis stone-associated particulate organic material was the single best predictor (r^2 = 0.57) (Table 7.3). This appears

Table 7.2. Correlation (r) of principal axis one, two and three with a number of biological, hydrological and chemical parameters. * indicates significant correlations at $P = 0.05$.

Physicochemical/ Biological parameter	Axis one	Axis two	Axis three
BIOLOGICAL			
Epilithic pigment conc.	0.71*	0.04	-0.18
Epilithic carbon conc.	0.73*	0.15	0.30*
Coarse POM	-0.25	0.48*	0.19
Fine POM	-0.16	0.42*	0.17
Total POM	-0.27	0.55*	0.19
Stone POM	0.15	0.76*	0.18
CHEMICAL			
Spot conductivity	0.04	0.18	0.34*
Spot pH	-0.05	0.21	0.27
Mean conductivity	-0.19	0.48*	0.43*
Mean pH	-0.36*	0.27	0.14
Mean alkalinity	0.04	0.45	0.49
PHYSICAL			
Spot current velocity	-0.05	-0.42*	-0.14
Spot depth	-0.14	-0.45*	0.14
Spot temperature	0.17	-0.19	0.19
Mean current velocity	0.04	-0.60*	0.08
Mean depth	-0.04	-0.60*	0.20
Mean temperature	-0.14	-0.62*	0.33
STABILITY			
Spot temperature range	-0.48*	-0.37*	0.01
Mean temperature range	-0.69*	-0.47*	0.09
Current variation	-0.18	-0.73*	0.01
Depth variation	-0.42*	-0.38*	-0.14
Spot stone movement	-0.48*	-0.32*	-0.24
Mean stone movement	-0.50*	-0.35*	-0.25
Pfankuch bottom component	-0.79*	-0.19	-0.13
Tractive force	-0.08	-0.48*	-0.58*
Overall stability	-0.59*	-0.43*	-0.14

to reflect an ordination from open to forested sites along axis two. Axis three appeared to separate Grasmere Stream from the other sites (Fig. 7.3), and while some physicochemical factors are weakly associated with this (Table 7.2), it is more probably a consequence of the site being the only lake outflow.

A particular suite of taxa was associated with each of the axes (and its associated environmental variables) and are presented in Table 7.4. Axis one was posi-

Table 7.3. Results of a stepwise regression analysis of principal axes one, two and three against 26 biological, physicochemical and stability measurements. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Parameter estimate	Partial r^2	Model r^2
PRINCIPAL AXIS ONE			
Intercept	14.11		
Pfankuch bottom component	-0.40	0.62	0.62
Current variation	0.18	0.12	0.74
Epilithic pigment conc.	0.30	0.08	0.82
Epilithic carbon conc.	0.14	0.03	0.85
Mean alkalinity	-0.13	0.03	0.88
Mean temperature range	-0.37	0.02	0.90
Stone POM	0.10	0.01	0.91
PRINCIPAL AXIS TWO			
Intercept	-5.30		
Stone POM	0.26	0.57	0.57
Current variation	-0.18	0.14	0.71
Tractive force	0.05	0.10	0.81
Fine POM	3.84	0.03	0.84
Pfankuch bottom component	0.10	0.01	0.86
Spot conductivity	0.01	0.01	0.87
PRINCIPAL AXIS THREE			
Intercept	1.81		
Tractive force	-0.12	0.33	0.33
Mean conductivity	0.07	0.32	0.66

tively associated with taxa commonly, or exclusively found in more stable streams, which were also streams that had the highest epilithic biomass. Axis two taxa were associated with forest streams, whereas the taxa associated with axis three essentially characterised Grasmere Stream.

Analysis of patterns in community structure in each season, when examined separately, revealed similar trends to those observed for the annual means or combined data sets. However, the axes did not always correlate with the same environmental variables.

The cluster dendrograms obtained with mean annual data using the four different distance measures are plotted in Fig. 7.4. Each of the distance measures produced a slightly different grouping of sites, although they all showed the same overall trends. In fact three of the measures at an average distance between clus-

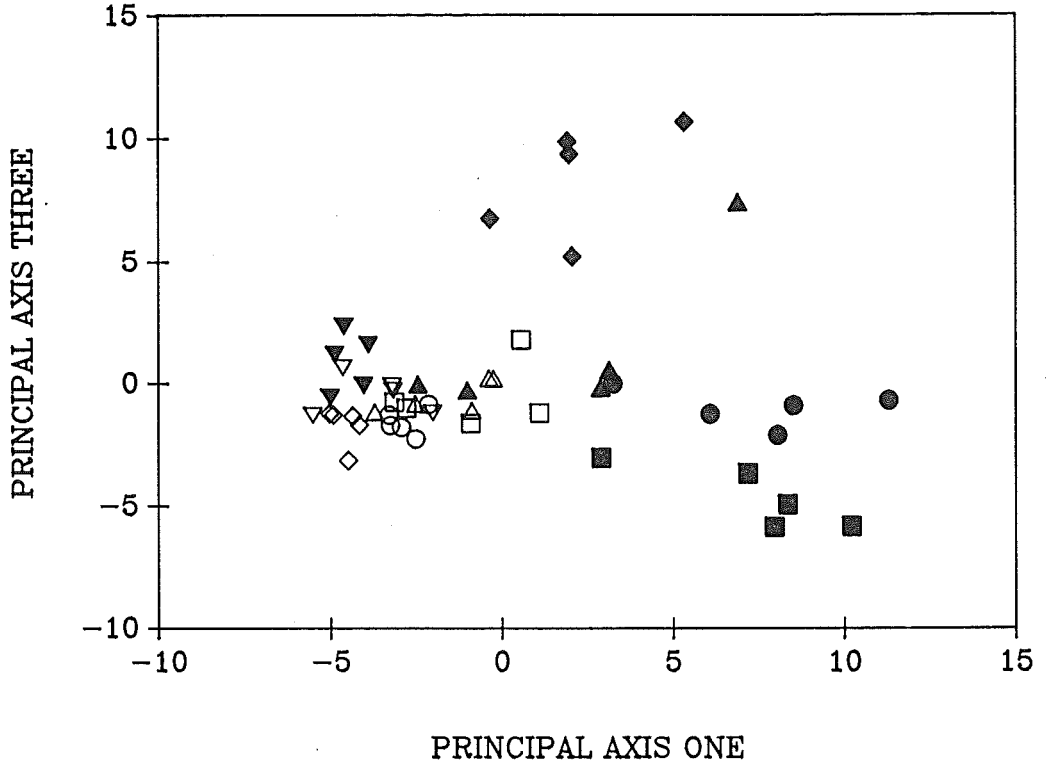


Figure 7.3. Principal axis three as a function of principal axis one for invertebrate communities of the ten streams in five seasons. Symbols as for Fig. 7.1.

ters of about one, had a pattern that was, with the exception of Bruce Stream in the Bray-Curtis dendrogram, identical. However, the analysis using the relative abundance distance measure, produced a somewhat different pattern to the other three, with a pattern that mirrored the overall stability of the sites more closely.

Table 7.4. Taxa associated with each of three axes from a principal components analysis of community composition of my study sites.

Axis 1	Axis 2	Axis 3
Austrosimulium laticorne	*Cristaperla fimbria*	*Aoteapsyche colonica*
early instar Hyrobiosidae	Empididae sp. B	*Aphrophilia neozelandica*
Harpactacoid Copepoda	Ostracoda sp. A	Chydoridae sp.
Hudsonema aliena	*Hydrobiosella stenocerca*	*Coloburiscus humeralis*
Hydrobiosis parumbripennis	Macropelopiini sp.	Cyclopoid Copepoda
Hydridae sp. A	*Paucispinigera* sp.	Elmidae sp. A
Limnophora sp. A	*Neppia montana*	*Hudsonema amabilis*
Maoridiamesa harrisi	*Zelandopsyche ingens*	*Neurochorema confusum*
Orthocladiinae sp. B	*Philorethrius agilis*	*Olinga feredayi*
Hydrachenellae sp. A	*Spaniocerca zelandica*	*Physa* sp.
?*Rheocricotopus* sp.	*Stenoperla macllelani*	*Psilochorema nemorale*
Oligochaeta sp.	*Orchymontia spinipennis*	*Pycnocentria evecta*
Oxeythira albiceps	*Homolaena spatulata*	*Eiseniella tetraedra*
Potamopyrgus antipodarum		
Tardigrada		
Rhabdocoela		

All the unstable sites were grouped together, and the other sites were split into three groups of similar and increasing stability. They were Middle Bush, Grasmere Stream and Porter River (overall stability score = 0.59-0.83), Cora Lynn and Lake Grasmere (overall stability = 0.51-0.52) and Slip Spring (overall stability = 0.39).

In the other three dendrograms, the four open unstable sites were also consistently grouped together, except that the Bray-Curtis measure isolated Bruce Stream, the most unstable site. Furthermore, as in the ordination analysis, the

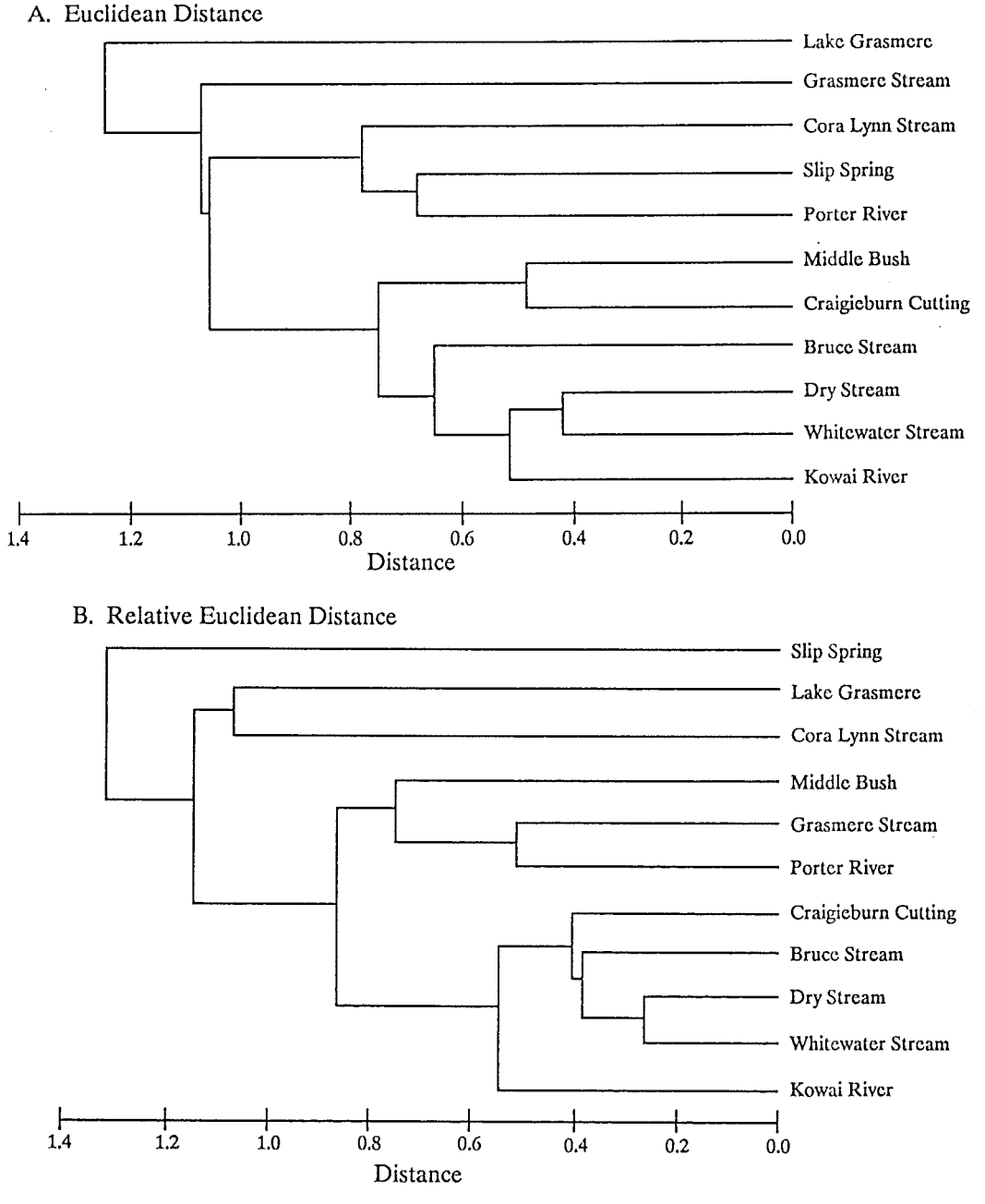
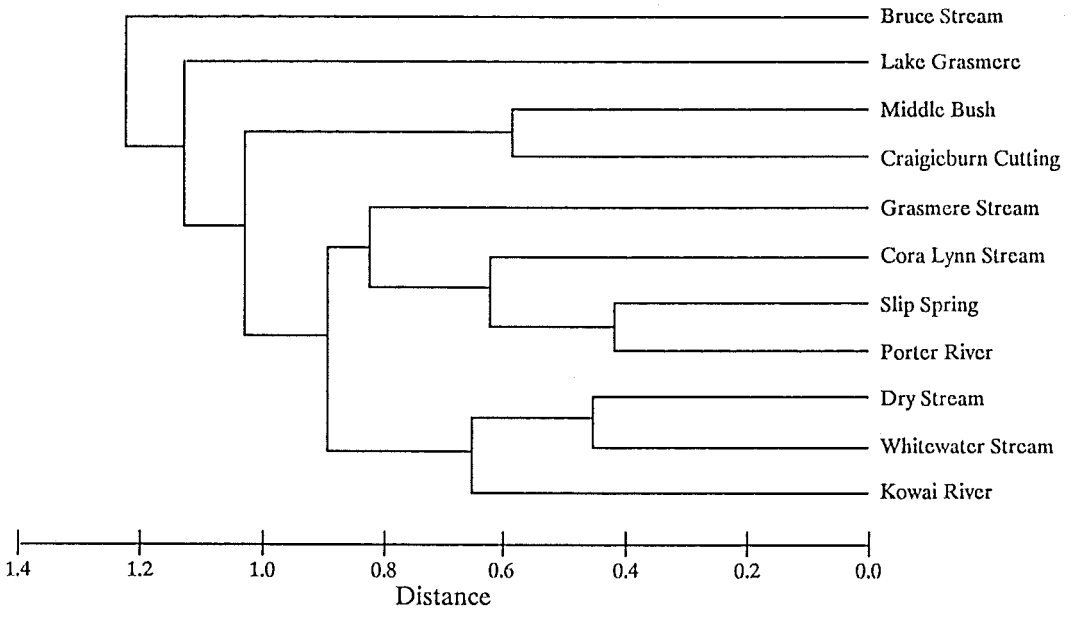


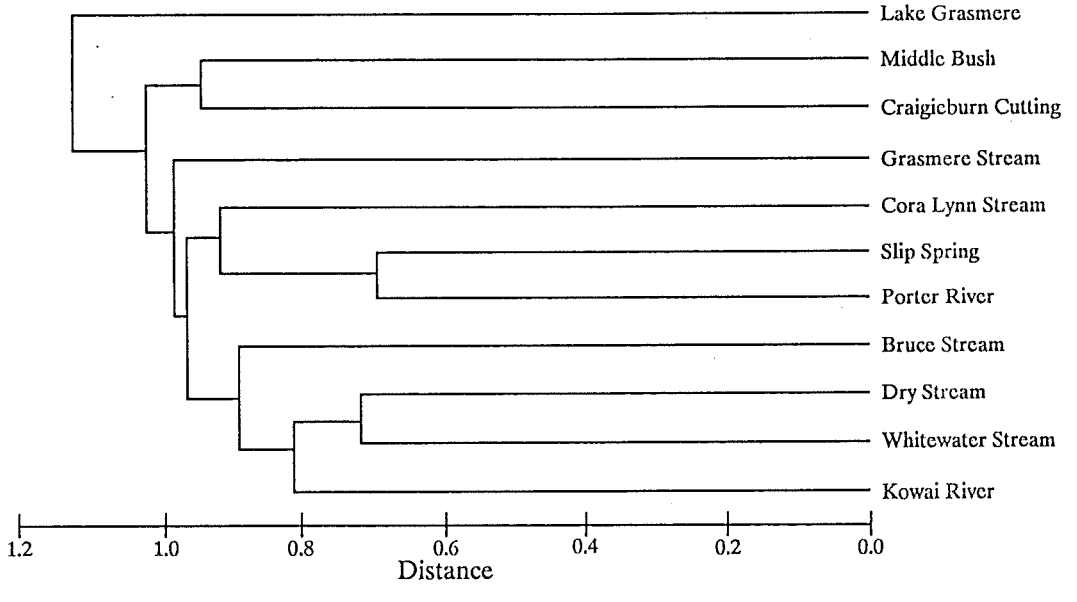
Figure 7.4. (*Continued on following page*) Clustering of the invertebrate communities of the study sites based on mean abundance data (five seasonal data sets averaged). All dendrograms are constructed with the average linkage clustering algorithm. Distance measures used are Euclidean (A), relative Euclidean (B), Bray-Curtis (C) and presence/absence Euclidean (D).

Figure 7.4. (*Continued*)

C. Bray-Curtis Distance



D. Presence/Absence Euclidean Distance



two forest sites, Middle Bush and Craigieburn Cutting, were grouped together with all three measures. On the basis of absolute densities (i.e., Euclidean distance) the two forest sites were also closely linked with the open unstable sites. All of these sites shared comparatively low densities, although species composition differed somewhat so that the distance measures that emphasised community composition (e.g., presence/absence) grouped the forest sites separately from the rest. Lake Grasmere was separated from most of the other sites either as an outlier or in an outlying group, and Grasmere Stream was also isolated but with vary-

ing distance from the other site groups depending on the distance measure used. Porter River, Slip Spring and Cora Lynn, all open stable sites, were also consistently grouped together.

Analysis carried out with data for each of the seasons separately, produced similar but not identical results to those recorded above. Analysis of all the seasonal samples together (using relative Euclidean distance) produced five distinct groups. The first three of these consisted of the five seasonal samples from Lake Grasmere, Cora Lynn and Slip Spring, respectively. They were the three most stable sites and it appears that each is more similar to itself, than to any other site at all times. The other two groups were respectively, all the unstable sites, and the three remaining stable sites (Porter River, Middle Bush and Grasmere Stream), although four samples from the former group were clustered with the latter. Within each of these groups the seasonal samples taken from a particular site did not always cluster closest to each other, and nor were seasonal samples consistently grouped. It appears therefore that at the unstable sites, Porter River, Middle Bush and Grasmere Stream neither season nor the intrinsic nature of the site, was underlying the similarity of their communities.

DISCUSSION

The "common core" of invertebrate taxa found in streams in a number of other New Zealand studies (e.g., Rounick & Winterbourn, 1982; Graesser, 1988; Quinn & Hickey, 1990a) were also present in the Waimakariri River Basin streams, although they were not always the dominant community members. Many invertebrates, particularly the more common species, were collected at several if not all the sites; however, their relative abundance and density differed among sites. This is consistent with the findings of several other workers, that many New Zealand benthic invertebrate species are present over a wide range of physicochemical conditions and wide geographic area (e.g., Quinn & Hickey, 1990a) but that their relative abundances are controlled by one or more underlying factors, such as stability. Many New Zealand stream invertebrates appear to have generalised feeding habits, broad habitat requirements and rapid colonising abilities (Cowie, 1985; Winterbourn, 1986), and the physicochemical nature of a stream consequently places little or no constraint upon their ability to colonise, but does appear to affect their relative success (i.e., how many individuals of each taxon colonise a particular stream and how long they remain there).

Two factors seem to be approximately equally important in determining observed differences in the density and relative abundance of taxa among my study

sites. The first of these was environmental stability, and all the unstable sites had similar faunas dominated by *Deleatidium* sp., *Slavina* sp., *Austrosimulium alveolatum* and three species of chironomid. Although these taxa were also present at many of the stable sites, communities at the latter were generally dominated by other taxa. Even Craigieburn Cutting (the unstable forest site), despite having a fauna similar to that of Middle Bush (the other forest site), tended to have taxa and densities more similar to those at the other unstable sites (although the exact nature of this relationship seemed to fluctuate with the seasons (and presumably stability)). The taxa present at the unstable sites probably reflect those that are little affected by physical disturbances or that can recolonise rapidly following a disturbance, and have been recorded in other studies as taxa that are both resilient and persistent in the face of flooding (Sagar, 1986; Scrimgeour *et al.*, 1988; Scrimgeour & Winterbourn, 1989).

Differences in the communities of stable sites were far greater than those observed between unstable sites, and this reflects the other important factor influencing community structure; namely, the specific nature of the site (i.e., open, forested, lake outlet, lake shore). This factor had a pronounced effect on community structure at the stable sites, such that differences in communities between sites were as large as differences between each of them and the group of unstable sites. However, the effect of site-specific influences seemed to be restricted to the presence or absence of particular taxa and/or their densities, whereas differences in the relative abundance of species appeared to be more closely linked to stability than to the intrinsic nature of the stream.

Therefore in summary, over the narrow physicochemical and geographic range of the study sites, stability seemed to be the primary force structuring benthic invertebrate communities. Thus, if environmental conditions are highly unstable, a particular suite of species well adapted to surviving such conditions will be found. However, if conditions are relatively stable, these species, although still present, are no longer the dominant community members. The particular suite of species that becomes dominant will in turn be dictated by the specific nature of the stream, that is, whether it is forested or open, a lake shore or a lake outlet.

CHAPTER 8

COMMUNITY STABILITY: PERSISTENCE

INTRODUCTION

The relationship between structure and stability in communities has been a central theme in ecology since it was introduced by Elton and MacArthur in the 1950s and 60s (MacArthur, 1955; Elton, 1958). Since that time, the topic has received considerable attention from theoretical ecologists (for reviews see May, 1981; Pimm, 1982; Chesson, 1986; Chesson & Case, 1986), but very little empirical data appear to have been collected about the stability of real communities (Hildrew & Townsend, 1987; Townsend *et al.*, 1987).

The accomplishment of such studies is, however, complicated by the multitude of parameters associated with the concept of stability (for reviews see Harrison, 1979; Connell & Sousa, 1983). "Persistence" has been used by many to describe the ability of a system to remain in a relatively constant state over time (Lewontin, 1969; Holling, 1973; Webster *et al.*, 1975; Harrison, 1979; Grossman, 1982; Lake & Barmuta, 1986). Persistence may be maintained in a community by a lack of any disturbing influence, or conversely by either of the other two parameters commonly associated with stability. These are "resistance", the ability of a community to resist or remain unchanged by a disturbance (Webster *et al.*, 1975; Harrison, 1979; Connell & Sousa, 1983; Lake & Barmuta, 1986), and "resilience", the ability of a community to return to its original state following a disturbance (Webster *et al.*, 1975; Harrison, 1979; Grossman, 1982; Connell & Sousa, 1983; Lake & Barmuta, 1986).

Grossman (1982) suggested that the stability of the environment would affect the processes controlling community structure and that this in turn would affect community persistence. Communities in constant or regularly fluctuating habitats should be regulated by deterministic (or equilibrium) processes (e.g., competition and predation) and have a highly predictable structure (i.e., high persistence) (Harrison, 1979; Sousa, 1979; Grossman, 1982). In contrast, communities in highly unpredictable environments should be more strongly influenced by stochastic processes. In other words assemblage structure will be determined largely by unpredictable environmental changes, rather than through biological interactions, although the latter may still occur (Sale, 1977, 1980b). Assemblage structure in unpredictable environments will consequently be unpredictable and have low persistence (Grossman, 1982).

Grossman (1982) concluded that the structure of fish communities in intertidal rock pools was consistent with a deterministic model of community organisation. He found that fish communities were highly persistent in time, despite his constant removal of fish from the rock pools. As he considered that deterministic communities are characteristic of constant or regularly fluctuating habitats, the removal of fish in this case presumably represented a "regular" disturbance. Townsend *et al.* (1987) and Lake & Barmuta (1986), in contrast, claimed that communities which persist in variable environments may be controlled more by deterministic processes than do those whose structures change markedly. As communities can persist in the face of disturbances through possessing high resistance or resilience, it does not necessarily follow that communities in randomly fluctuating environments have low persistence.

In the last chapter, I examined the influence of environmental stability on the composition of invertebrate communities at my study sites (i.e., what particular species were present). In this chapter I consider the effect of environmental stability on the persistence of those communities, and in particular whether communities in the unstable streams exhibit a similar degree of constancy to those in the stable streams.

MATERIALS AND METHODS

The seasonal constancy of three components of the benthic invertebrate communities collected at each of the sites (Appendix I) was examined (i.e., samples collected in each of the seasons at one site were compared).

Assemblage structure (i.e., presence/absence of species) was examined with Cochran's Q test (Cochran, 1950). This test compares the observed variance in total numbers of taxa among seasons with the variance expected if taxa are randomly distributed among seasons, when the data are in the form of dichotomized ordinal information, i.e., a taxon is either present or absent (Pridmore, 1985).

The degree of constancy of invertebrate densities was assessed with Kendall's coefficient of concordance (W) (Siegel, 1956). This is a non-parametric technique of multiple rank correlation, and therefore the constancy of densities *per se* was not examined, instead the constancy of the rank position of a particular taxon in terms of its density was compared between seasons. Analysis was carried out using both the ten most abundant taxa at each site, and all common taxa (defined as those with densities greater than 1% of the total). Changes in actual densities were assessed by calculating the Euclidean distance between each pair of consecutive seasonal samples.

Changes in relative abundance were analyzed by measuring multivariate distances between consecutive seasons. Bray-Curtis (Bray & Curtis, 1957), relative Euclidean and chord distance (Pielou, 1984) measures were used. All three essentially examine the similarity of relative abundances in multivariate data sets and have been recommended as suitable for use with ecological data sets in a number of reviews (e.g., Beals, 1984; Ludwig & Reynolds, 1988).

RESULTS

Results of the Cochran's Q test are given in Table 8.1. All but one unstable site (Kowai River) had significantly different faunal assemblages across the five seasonal samples, whereas four of the six stable sites did not exhibit significant changes in species presence/absence. The significant change in species presence/absence at Slip Spring could be attributed to the first spring sample, which was taken 20 weeks after a severe disturbance from cattle grazing (see Appendix III); removal of this sample yielded a Cochran Q value of 5.74 ($P > 0.05$), indicating that communities may have not fully recovered. The only other stable site to exhibit a significant seasonal change in faunal assemblage was Cora Lynn, and this change could also be attributed to a disturbance event. Although normally a very stable site with relatively constant flow, it received water from a previously dry waterfall during a period of "unusually" high rainfall (this rainfall resulted in

Table 8.1. Numbers of taxa and test statistics for Cochran's Q test, Kendall's coefficient of concordance for the ten most abundant taxa and for all common taxa (i.e., those with relative abundances greater than 1% of the total). Significant statistics (i.e., $P < 0.05$) are indicated by *.

SITES	Number of taxa	Cochran Q test	Number of taxa	Kendall's W for the top ten taxa	Number of taxa	Kendall's W for common taxa
UNSTABLE						
Kowai River	62	2.46	20	0.55*	24	0.56*
Whitewater Stream	58	30.82*	18	0.46*	21	0.51*
Dry Stream	69	18.01*	23	0.46*	23	0.46*
Craigieburn Cutting Stream	71	36.16*	24	0.38*	30	0.42*
Bruce Stream	43	18.19*	27	0.36*	27	0.34*
STABLE						
Porter River	77	9.25	17	0.62*	22	0.67*
Slip Spring	74	17.83*	13	0.66*	13	0.66*
Cora Lynn Stream	92	38.76*	22	0.51*	26	0.52
Middle Bush Stream	82	6.35	17	0.46*	29	0.64*
Grasmere Stream	80	3.91	21	0.53*	27	0.57*
Lake Grasmere	82	1.68	19	0.65*	18	0.67*

the flooding of Greymouth), which led to a marked increase in its discharge. This flow increase occurred prior to taking the last two samples, and removal of them from the analysis yielded a non significant Q value ($Q = 4.54, P > 0.05$).

Kendall's coefficient of concordance values for the top ten taxa at each site, and all common taxa, are listed in Table 8.1. All values were significant ($P < 0.05$) indicating that species ranks did not change significantly across the seasons. However, values for both sets of taxa decreased (indicating communities were less strongly correlated) as the stability of the site decreased (Fig. 8.1). This relationship was significant for the common taxa ($F = 8.64$, $df = 1,9$, $P < 0.05$,

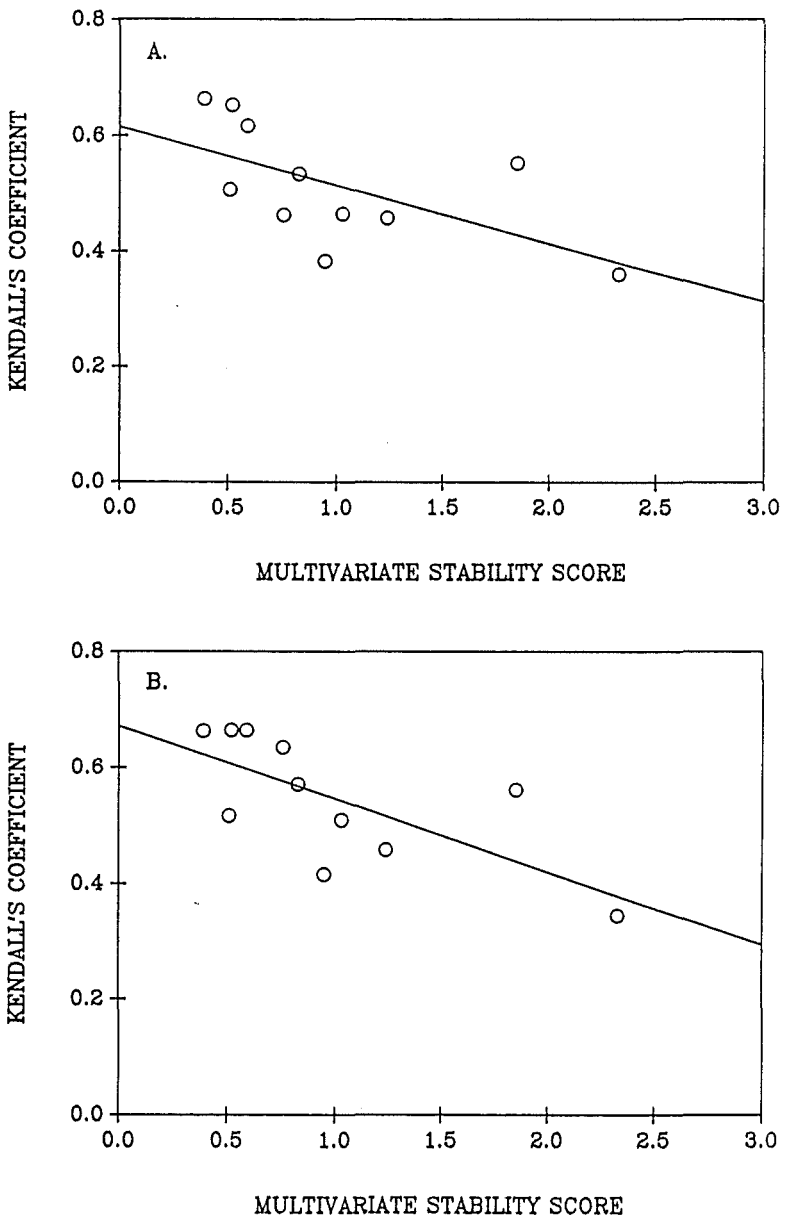


Figure 8.1. Kendall's coefficients of concordance (W) for A) the ten most abundant taxa and B) the common taxa as a function of overall stability (multivariate stability score). The equation for A) (excluding Kowai River and Bruce Stream) is $W = 0.72 - 0.26$(stability score), $r^2 = 0.57$ and for B) $W = 0.67 - 0.13$(stability score), $r^2 = 0.49$.

r^2 = 0.49), but was only significant for the top ten taxa if Kowai River and Bruce Stream (the two most unstable sites) were not included (F = 9.40, df = 1,7, $P < 0.05, r^2 = 0.57$).

Euclidean distances between seasonal samples actually decreased (Fig. 8.2) as stability of the sites declined (F = 21.66, df = 1,39, $P < 0.05, r^2 = 0.42$). However, although absolute changes in densities were higher at the more stable sites, this may have been because they had higher densities and consequently would have experienced larger absolute changes in animal numbers. The proportionate change in total density (as expressed by the coefficient of variation; see Chapter 5) increased as the sites became less stable.

Mean values for Bray-Curtis distance measures between consecutive seasons are plotted against stream stability in Fig. 8.3. They increased significantly (indicating larger seasonal changes) as the stability of the sites decreased (F = 10.47, df = 1,39, $P < 0.05$, r^2 = 0.32). Relative Euclidean and chord distances showed similar, but weaker trends.

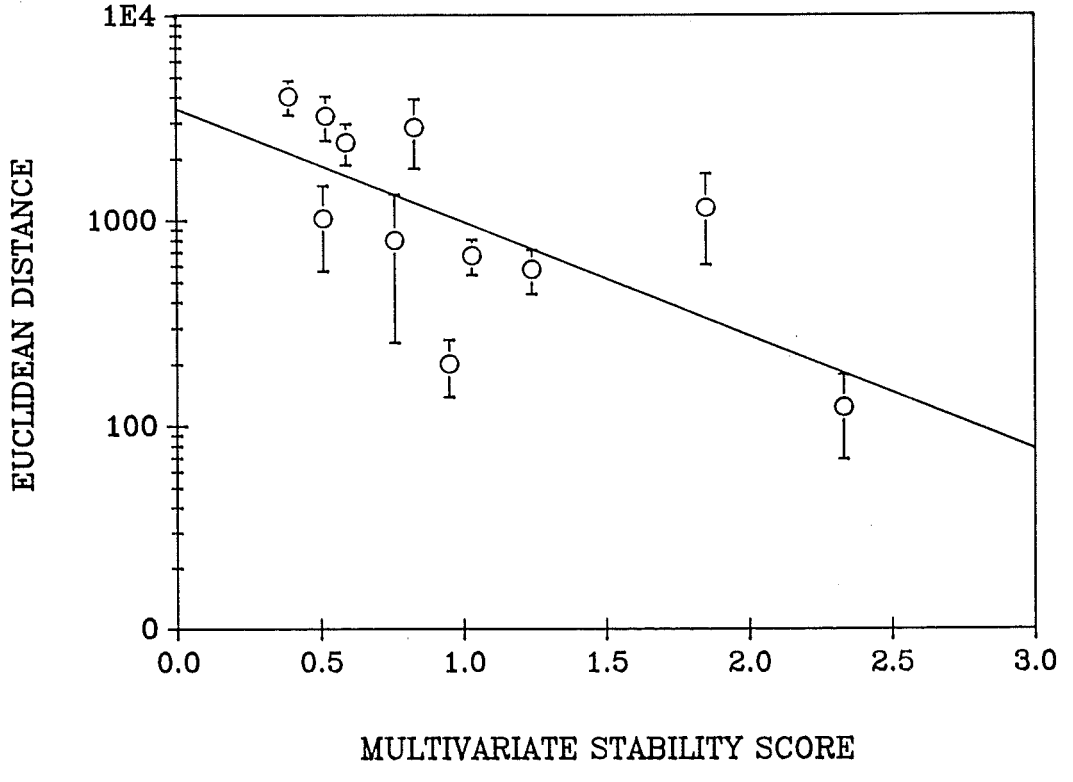


Figure 8.2. Average Euclidean distance between communities collected at each site in five consecutive seasons as a function of overall stability. Plotted values are averages ± 1 SE for the four seasonal comparisons. Regression analysis was performed on the entire data set to yield the equation, $\log_{10}$(Euclidean distance) = 3.14 - 0.59(stability score), r^2 = 0.42.

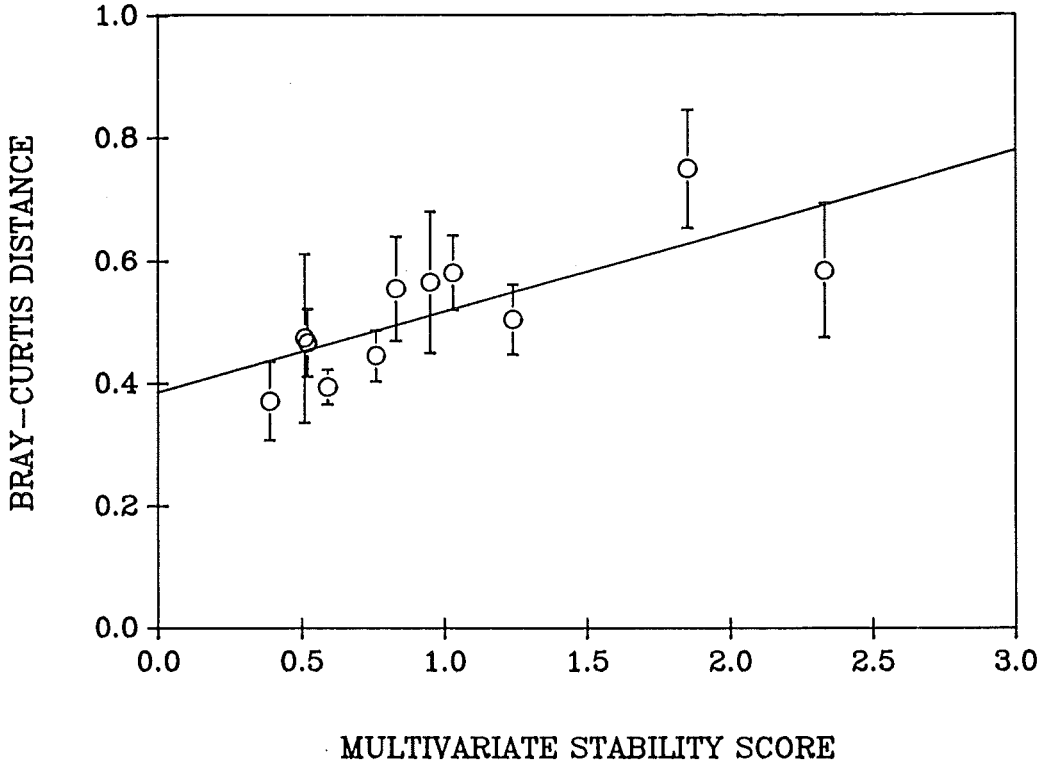


Figure 8.3. Average Bray-Curtis distance between communities collected at each site in five consecutive seasons as a function of overall stability. Plotted values are averages ± 1 SE for the four seasonal comparisons. Regression analysis was performed on the entire data set to yield, Bray-Curtis distance = 0.43 + 0.13(stability score), r^2 = 0.32.

DISCUSSION

My analyses indicate that stable sites generally have more persistent communities than do unstable sites. However, this is not necessarily so and it depends on just what aspect of a community one is examining. Rank abundances of common or dominant taxa showed no significant change across seasons at any of my sites, although there was a tendency for ranks at more stable sites to be more strongly correlated. This is consistent with the findings of Meffe & Minckley (1986) and Graesser (1988) who both found that rank abundance of common taxa in the invertebrate communities of a Sonoran Desert stream and four New Zealand West Coast streams respectively, was persistent over time. As both these studies were conducted in streams that could tentatively be classified as "unstable", it appears that neither life cycle changes nor disturbances lead to marked changes in the rank abundances of common taxa in any of these streams.

On the other hand, Townsend *et al.* (1987) found that species composition and relative abundance of the major species of invertebrates in 27 English streams differed markedly in two surveys made eight years apart. Connell & Sousa (1983) have argued that persistence can only be assessed when consecutive samplings are

far enough apart in time for populations to have turned over completely. The different time scales considered in the above studies (an 8 year interval c.f. < 1 year intervals) may account for the differences in conclusions. However, all of the studies encompassed time spans that would have allowed at least one generation of invertebrates to have matured and another to have appeared.

Although absolute changes in population sizes were greater at the more stable sites, this would be expected by chance simply because the population sizes were also greater. Both the proportionate changes in densities and the seasonal change in relative abundances were greater at the less stable sites. Therefore, given the difference in population sizes between stable and unstable sites, the variation in population size at the unstable sites would appear to be greater.

Analysis of species composition, where equal weight was given to rare and common taxa, revealed that most of the stable sites had highly persistent species composition, whereas unstable sites did not. Although they found a generally low level of persistence in their English streams, Townsend *et al.* (1987) did find higher persistence of species in streams with low discharge, cool temperatures and low, stable pH; my findings of higher persistence in environmentally stable sites, is at least consistent with this. Thus, it appears that the local extinction of rare species is more likely where the stream environment is relatively more changeable.

In summary then, it appears that the persistence of common taxa at all sites was generally high, although there was a trend for it to be higher at the more stable sites. However, relative abundance of species populations was more variable at the less stable sites, and persistence of the entire fauna (both rare and common species) was high only at the stable sites.

CHAPTER 9

COMMUNITY STABILITY: RESILIENCE

INTRODUCTION

In the last chapter I found that persistence, at least of the more common taxa, was relatively high at all study sites, although overall it was higher in the communities at the more stable sites. Persistence of communities at the stable sites can be easily explained, for provided biotic interactions are at or near equilibrium (e.g., species are not becoming extinct because of exclusion by competitive dominants) there are no external forces (such as flood events) that could lead to the extinction of species. However, this is not so for the unstable sites as many are constantly experiencing highly fluctuating discharges with associated disturbance of the substrata.

Persistence of communities in these unstable habitats can be attributed to one of two factors, either resistance to disturbance, or resilience following disturbance. Numerous studies (Siegfried & Knight, 1977; Fisher *et al.*, 1982; McElravy *et al.*, 1989; Sagar, 1986; Scrimgeour & Winterbourn, 1989) have shown that flood events result in a reduction of both density and diversity of invertebrate communities, but that they recover quickly following the disturbance. It seems then that as a general rule stream invertebrate communities recover from, rather than resist disturbances to their environment.

While stream ecologists seem to have been content with recording that stream invertebrate communities are affected by flood events and that they recover from these floods relatively quickly, the "rest" of ecology has been embroiled in a debate for the past forty years about what, if any, characteristics of a community (particularly its complexity) give it the ability to resist or recover from any such disturbance it may experience.

The "traditional" view of Elton (1958) and MacArthur (1955), held during the 1950s and 1960s, was that more complex communities were more stable. Elton's argument was based on a number of empirical and theoretical observations; namely, that island faunas are more vulnerable to invasion from introduced species than are their continental counterparts, crop monocultures are particularly vulnerable to pest outbreaks, species-rich tropical communities are not known for large population fluctuations, simple laboratory communities are difficult to maintain, and mathematical models of interactions between two species are inherently unstable. MacArthur (1955) also suggested that the more possible en-

ergy pathways in a community (i.e., the more complex they are) the less likely were the densities of the constituent species to fluctuate in response to changes in the densities of other species. However, these ideas now appear to have been largely discredited as a basis for believing that more complex communities should be more stable (Begon *et al.*, 1990).

During the 1970s, this "traditional" view was challenged by the use of mathematical models and stability analysis of theoretically derived systems (for a review see May, 1981). Surprisingly perhaps, the results of this work suggested that the converse viewpoint was more likely, that is, more complex communities were less stable than simple ones (Gardner & Ashby, 1970; May, 1972, 1973). Many of these mathematical studies were based on models of Liapunov functions[1] which examine the local stability of matrices (in ecological applications the matrix is known as the community matrix); local stability being defined as the tendency of a system to return to its original state following a small disturbance. Local stability can be assessed by examining the eigenvalues[2] of the matrix. If they fall within certain constraints (these depend on the underlying structure of the matrix), the matrix will be stable (i.e., return to its original state following a small disturbance), otherwise the system will be unstable and move to another point in mathematical hyperspace following any small disturbance. However, the situation changes if global (i.e., stability in the face of large disturbances) rather than local stability is considered. For example, Pimm (1979a) modelled the removal of a species from a community and examined the effect of this on the stability of the community. He found that stability actually increased with increasing complexity but only if basal species (i.e., those at the bottom of the food chain) were removed; it decreased if top predators were removed. Similarly, stability may be unaffected or may increase with complexity if the system being considered is a "donor-controlled" system (i.e., the food supply influences the consumer population but is not itself affected by the consumers) (DeAngelis, 1975). Finally, Pimm (1979b) found that if only communities with a stable structure are considered, then resilience will also increase with an increase in complexity.

While mathematical and theoretical studies of community stability and complexity have been prolific, there appear to be have been very few comparable,

1. Liapunov (1907) devised a method for examining the stability of a system of differential equations, without needing to solve the equations. This involved examining the trajectory of a function describing the system of equations, such that a function with a trajectory that spirals towards zero is stable. Functions with this property are known as Liapunov functions (see Barnett & Storey, 1970).

2. An eigenvalue is a property of all square matrices (i.e., the number of columns = the number of rows) such that A.x = lamba.x, where A is an n by n matrix, lambda is an eigenvalue and x is its corresponding eigenvector. Thus if a matrix A can be factorised into two matrices (i.e., A = B . C) so that one contains all zeros except on the diagonal, the diagonal entries are the eigenvalues and the columns of the other matrix are their corresponding eigenvectors.

empirical studies on real communities. May's (1972) original work involved examining the effect of three components of complexity (S (the number of species), C (the proportion of species interactions to possible interactions) and i (the average strength of these interactions)), on community stability. He found that communities would only be stable if $i(SC)^{1/2} < 1$, and much subsequent empirical work has centred around investigating the applicability of this inequality to real communities. In a number of studies (McNaughton, 1978; Rejmanek & Stary, 1979; Yodzis, 1980; Pimm, 1982; Briand, 1983; Cohen *et al.*, 1985) it has been found that S and C are inversely related (a requirement for stability if interaction strength remains constant), although Bruns *et al.* (1982), Bruns & Minshall (1983) and Winemiller (1989) have found the opposite for filter feeding invertebrates, predatory invertebrate communities and tropical stream fish, respectively.

As the mathematical modelling studies (e.g., Gardner & Ashby, 1970; May, 1972, 1973) indicate that less complex communities will have greater resilience (i.e., be more stable) then for a given number of species, connectance should be lower in more unstable habitats. There is some support for this (Briand, 1983; Cohen *et al.*, 1985) although the assessment of environmental stability in these studies was very subjective (Lawton, 1989).

Several workers have also constructed community matrices and examined the eigenvalues of these matrices to determine if the communities would in theory, be able to recover from a small disturbance. Lawlor (1980a) examined empirical data on bird (Cody, 1974) and lizard (Pianka, 1967) assemblages, and found that resilience (measured as the minimum eigenvalue of the community matrix) was inversely related to species richness, although it was consistently higher than that in analogous random communities. Similarly, Bruns *et al.* (1982) and Bruns & Minshall (1983) found that lotic filter feeding, grazing and predatory invertebrate communities exhibited inverse relationships between resilience and species richness.

Community matrices are composed of elements that represent the effect of each species on each other species in the community. Entries may be zero (no effect), negative (e.g., competitive) or positive (e.g., mutualistic). Often the matrices are constructed on the basis of competitive interactions and consequently their elements are frequently termed competition coefficients. Several of the studies mentioned above (e.g., Bruns *et al.*, 1982; Bruns & Minshall, 1983) and others (e.g., Levins, 1968; MacArthur, 1968; Levins *et al.*, 1973; Culver, 1974) have evaluated these competition coefficients by examining resource overlap. The link between resource overlap and competitive interaction is rather tenuous however, and although several techniques for relating the two have emerged (e.g.,

MacArthur & Levins, 1967; Schoener, 1974; Crowell & Pimm, 1976), there does not appear to be any "perfect" substitute for examining population interactions experimentally (Rosenzweig *et al.*, 1985). While it may be possible to determine interaction terms experimentally for small communities, and has been accomplished successfully for both water-filled *Heliconia* bract-insect communities (Seifert & Seifert, 1976) and simple planktonic communities (Levitan, 1987), it rapidly becomes impractical as the community becomes larger. It also becomes increasingly difficult to evaluate secondary effects of other species on those interactions (e.g., species A keeps the population of species B so low that it does not affect species C which otherwise it would do). Thus, although construction of community matrices using resource overlap data is by no means the perfect solution, it does at least serve as an approximation, albeit a rough one, for examining the question of community stability (Lawlor, 1980a; Bruns & Minshall, 1983; Pimm, 1985).

In this chapter, I consider the resilience of community matrices constructed for samples collected at each of my study sites, by examining their eigenvalues. My initial hypothesis was that communities in the more unstable sites would have a greater resilience in order to persist in the face of continual disturbance. I also investigate how this resilience relates to the complexity of each community and the stability of the habitat in which that community occurred.

MATERIALS AND METHODS

I used the technique outlined by Bruns & Minshall (1983) for calculating the interaction terms for the community matrix. Thus, pairwise Spearman rank correlations for each species in the community were calculated for the fifteen stone samples collected at each of my sites (see Chapter 4). To avoid possible distortions inherent in this form of analysis, any species represented by only one individual was omitted (rare species are unlikely to have a significant effect on community stability anyway) and any double-zero matches were eliminated (Legendre & Legendre, 1983).

Non-significant correlations were given interaction terms of zero. Negative correlations (except those between predators and prey) were taken to represent competitive interactions. Schluter (1984, Table 4) listed the possible ecological basis of negative and positive associations of species on a resource state (in this case stones), and while it is possible that both negative and positive associations may be the result of competition there seems to be some evidence to suggest that the former is the case in at least some stream communities. Dudley *et al.* (1990) examined both habitat overlap and the nature of the competitive interaction

between *Blepharicera micheneri* and *Simulium virgatum* in a Californian stream and found that the two were negatively correlated in their occupation of habitat patches as a result of competitive dominance by *S. virgatum*. Other studies have also found that densities of a number of stream invertebrates are negatively correlated as a result of competition for both food (e.g., McAuliffe, 1984a; Hawkins & Furnish, 1987) and space (e.g., McAuliffe, 1984b; Hart, 1985; Hemphill, 1988). Schluter (1984) claimed a positive association may result from competition if competitors fluctuate in unison with their resources, however, if this were the case, competitors are unlikely to be having a strong effect on each other, as eventually one or the other should be excluded from the resource as in the case of *B. micheneri* and *S. virgatum*. Therefore I took positive associations (except those between predators and prey) to represent weak or nil interactions and ascribed a value of zero to them. Significant associations between predators and prey on the stones were attributed to the effects of one feeding on the other and not to an interaction for spatial resources. Thus, the predator was given a positive interaction term and the prey a negative interaction term. The sizes of the interaction terms were determined by the size of the correlation coefficients. Diagonal entries in the matrix (i.e., intraspecific interactions) were set to -1 following Pimm (1982).

Eigenvalues for each of the matrices were then extracted using PC-Matlab (Moler *et al.*, 1987).

RESULTS

Correlation analysis

The number of significant positive and negative correlations recorded in each season at my study sites are recorded in Table 9.1 along with the number of correlations (both positive and negative) that could be expected by chance. In all but two cases more correlations were recorded than would be expected by chance. Most sites had more negative than positive correlations, although there was considerable variation across the seasons. Porter River, Slip Spring, Grasmere Stream and Lake Grasmere, all stable sites, in general had more positive than negative correlations, however.

The number of significant correlations that occurred between predators and prey are also shown in Table 9.1. The vast majority of these were positive.

Community matrices

As most matrices were asymmetrical some of the eigenvalues associated with

Table 9.1. Number of significant correlations ($P < 0.05$) for all species collected in fifteen stone samples at each of my study sites.

Site	species	signif. positive correl.s	signif. negative correl.s	Number of expected by chance	predator species	signif. positive pred/prey correl.s	signif. negative pred/prey correl.s
UNSTABLE SITES							
KOWAI RIVER							
spring 1	22	51	15	11.6	6	19	1
summer	17	4	25	6.8	4	0	5
autumn	23	18	39	12.7	5	3	5
winter	19	1	36	8.6	2	0	6
spring 2	14	4	17	4.6	2	2	5
mean	19	15.60	26.40	8.82	3.80	4.80	4.40
SE	1.64	9.33	4.85	1.49	0.80	3.60	0.87
WHITEWATER STREAM							
spring 1	29	25	38	20.3	5	5	2
summer	28	23	42	18.9	9	7	5
autumn	27	18	31	17.6	6	7	3
winter	20	17	19	9.5	4	2	4
spring 2	9	2	1	1.8	0	0	0
mean	22.60	17	26.20	13.61	4.80	4.20	2.80
SE	3.75	4.04	7.41	3.50	1.46	1.39	0.86
DRY STREAM							
spring 1	27	28	32	17.6	8	10	8
summer	31	75	12	23.3	6	18	2
autumn	30	51	22	21.8	9	13	6
winter	19	12	5	8.6	5	4	0
spring 2	15	2	15	5.3	0	0	0
mean	24.40	33.60	17.20	15.27	5.60	9	3.20
SE	3.16	13.25	4.60	3.58	1.57	3.19	1.62
CRAIGIEBURN CUTTING STREAM							
spring 1	34	32	46	28.1	9	6	4
summer	27	10	45	17.6	6	1	7
autumn	27	15	38	17.6	7	2	2
winter	5	0	0	0.5	1	0	0
spring 2	8	0	7	1.4	1	0	0
mean	20.20	11.40	27.20	13.01	4.80	1.80	2.60
SE	5.76	5.91	9.84	5.29	1.62	1.11	1.33

Table 9.1. (*Continued on following pages*)

Table 9.1. (*Continued*)

BRUCE STREAM							
spring 1	14	3	19	4.6	1	0	0
summer	11	0	11	2.85	2	0	1
autumn	8	1	4	1.4	1	0	1
winter	2	0	0	0.1	0	0	0
spring 2	4	0	3	0.3	0	0	0
mean	7.80	0.80	7.40	1.81	0.80	0	0.40
SE	2.20	0.58	3.41	0.83	0.37	0	0.24
STABLE SITES							
PORTER RIVER							
spring 1	44	106	40	47.3	11	14	3
summer	43	152	56	45.2	11	32	9
autumn	47	242	61	54.1	13	31	4
winter	44	146	59	47.3	13	24	11
spring 2	34	33	7	28.1	7	6	0
mean	42.40	135.80	44.60	44.37	11	21.40	5.40
SE	2.20	33.99	10.10	4.35	1.10	5.02	2.01
SLIP SPRING							
spring 1	29	40	37	20.3	8	7	6
summer	44	91	65	47.3	14	19	5
autumn	41	45	105	41	12	9	20
winter	40	84	39	39	12	16	9
spring 2	43	85	52	45.2	13	19	9
mean	39.40	69	59.60	38.55	11.80	14	9.80
SE	2.69	10.91	12.42	4.79	1.02	2.53	2.67
CORA LYNN STREAM							
spring 1	46	74	170	51.8	12	13	21
summer	41	82	76	41	8	9	7
autumn	50	40	133	61.3	10	2	16
winter	30	35	55	21.8	3	2	1
spring 2	21	4	46	10.5	2	0	0
mean	37.60	47	96	37.25	7	5.20	9
SE	5.33	14.14	23.90	9.37	1.95	2.48	4.14
MIDDLE BUSH STREAM							
spring 1	38	22	86	35.2	6	2	6
summer	36	37	31	31.5	6	2	5
autumn	37	45	69	33.3	7	3	6
winter	34	34	39	28.1	5	0	3
spring 2	25	5	62	15	5	1	12
mean	34	28.60	57.40	28.60	5.80	1.60	6.40
SE	2.35	6.96	10.02	3.60	0.37	0.51	1.50

Table 9.1. (*Continued*)

GRASMERE STREAM							
spring 1	36	72	58	31.5	9	7	11
summer	41	200	29	41	13	33	3
autumn	32	65	37	24.8	6	14	3
winter	36	93	27	31.5	6	9	1
spring 2	33	43	62	26.4	5	7	3
mean	35.60	94.60	42.60	31.04	7.80	14	4.20
SE	1.57	27.53	7.33	2.83	1.46	4.92	1.74
LAKE GRASMERE							
spring 1	39	87	24	37.1	8	6	5
summer	38	60	48	35.2	11	9	6
autumn	44	110	122	47.3	12	14	33
winter	35	101	48	29.8	7	11	5
spring 2	36	88	55	31.5	6	8	5
mean	38.40	89.20	59.40	36.15	8.80	9.60	10.80
SE	1.57	8.46	16.51	3.07	1.16	1.36	5.55

them were conjugate eigenvalues (i.e., they had both real and imaginary parts). The imaginary parts of the eigenvalues indicate that the system oscillates (either away from or towards equilibrium) if disturbed (May, 1973; Pimm, 1982).

As I mentioned in the introduction, the constraints on the eigenvalues for stability differ depending on the underlying structure of the matrix, that is, whether the population growth models for the constituent species in the community are modelled better by differential or difference equations. Many insect populations, particularly those with distinct generations, are modelled best by difference equations (Hassell, 1979; Pimm, 1982). However, for them to be the most appropriate choice the time lag between generations needs to be relatively long (e.g., a year), so that the density of species in one year will depend on its interaction with other species in the previous year and not more recently (S.L. Pimm pers. comm.). It is unlikely that the time lag between successive generations of most New Zealand stream invertebrates is very long, as many exhibit poorly synchronised life histories and multiple generations (although the nature of life history patterns in New Zealand aquatic invertebrates is in general poorly understood). Most populations are probably modelled best by equations that lie somewhere in between difference and differential equations (Pimm, 1982), and the population dynamics of most New Zealand benthic invertebrates would seem to fall in line with this. Consequently, I considered stability criteria for both difference and differential equation based matrices, but as it turned out this made little difference to the interpretation.

For a differential based system the criterion for stability is that all eigenvalues have negative real parts, and for difference equation based systems the square of both the real and imaginary parts of all eigenvalues must be less than one (May, 1973). For simplicity I have ignored the imaginary parts of the eigenvalues in presenting the analysis, and this made no difference to the interpretation. The mean maximum and minimum eigenvalues (i.e., the real parts) are plotted in Fig. 9.1. All but two matrices (these only had intraspecific interaction terms) had eigenvalues outside the stability envelope of either type of equation. However, it is interesting to note that the more unstable sites had eigenvalues closer to the criterion for stability.

Given that only two of the matrices (and these have no interspecific interaction terms) are stable, it can be inferred that if disturbed all the communities would become extinct rather than returning to the status quo. Clearly, this does not happen. How then does the resilience of the communities compare if eigenvalues outside the stability criterion are ignored? Assessment of this again depends on the type of equations involved. For differential equations the return time is given by -1/(the real part of the largest eigenvalue) (Pimm & Lawton, 1977). Thus, the more negative the largest eigenvalue, the more rapidly will the

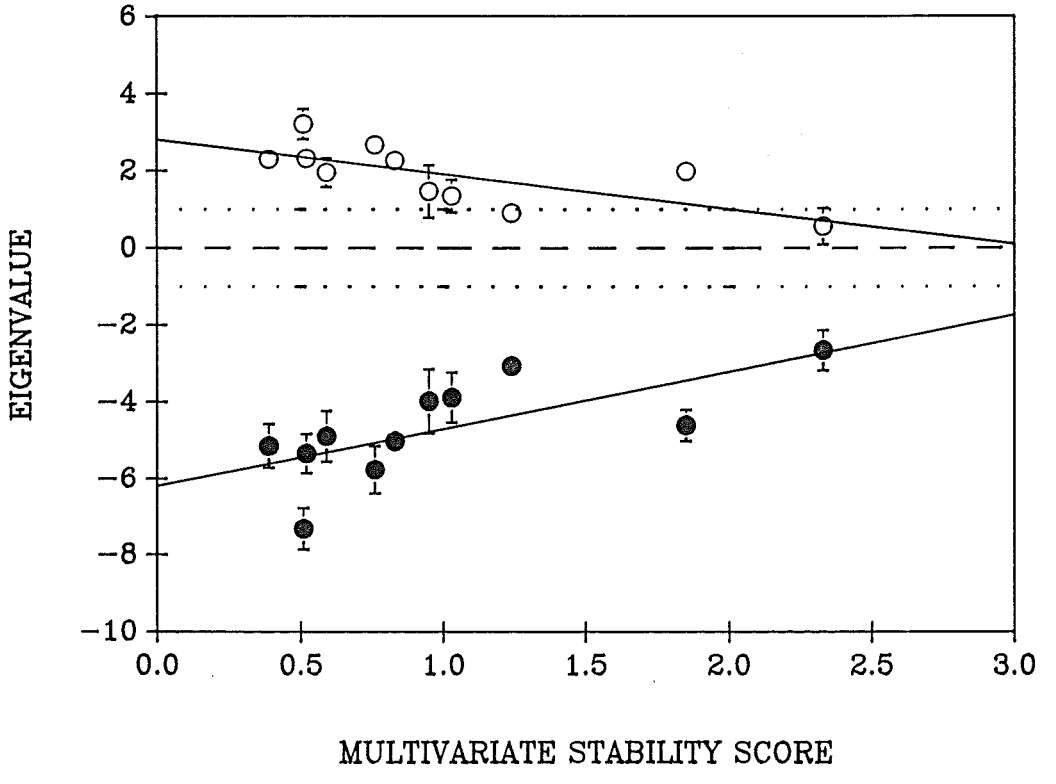


Figure 9.1. Mean maximum (o) and minimum (•) eigenvalues (± 1 SE) for community matrices collected at each of my study sites between October 1987 and October 1988, as a function of overall (multivariate) environmental stability. The area within the dotted lines is the stability criterion for matrices based on difference equations and the area below the dashed lines is the criterion for stability for a differential equation based system.

matrix return to its predisturbance state. For difference equation systems the smaller the dominant eigenvalue (the largest eigenvalue ignoring the sign) the more resilient the matrix (most advanced algebra texts e.g., Edelstein-Keshet, 1988; Fraleigh & Beauregard, 1989).

The measures of resilience for both equation types are plotted in Fig. 9.2. For both equation systems the matrices in the more unstable streams had greater resilience. The maximum eigenvalue (ignoring all positive eigenvalues) increased as overall (multivariate) environmental stability decreased (F = 4.55, df = 1,49,

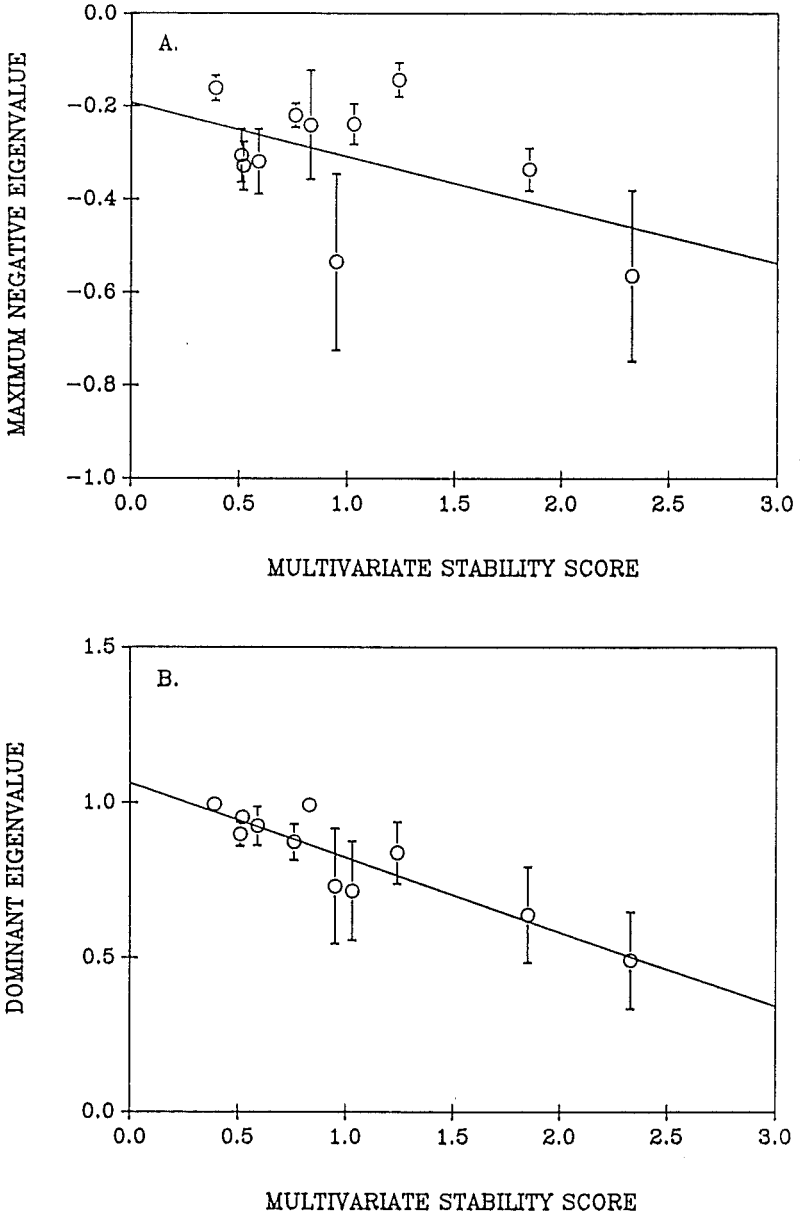


Figure 9.2. Mean maximum eigenvalue (A) (ignoring all positive eigenvalues) and mean dominant eigenvalue (B) (ignoring all those equal to or greater than one) as a function of overall environmental stability. Plotted values are averages of the seasonal means ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equations: maximum eigenvalue = -0.17 - 0.12(environmental stability score), r^2 = 0.11 and dominant eigenvalue = 0.97 - 0.24(environmental stability score), r^2 = 0.43.

$P < 0.05, r^2 = 0.11$), and the dominant eigenvalue (ignoring those greater than or equal to one) decreased as environmental stability decreased ($F = 23.65$, $df = 1,49, P < 0.05, r^2 = 0.43$).

What aspects of community structure may account for the increased resilience? Results of mathematical modelling suggest that communities in the more unstable streams (i.e., those with higher resilience) should be less complex (e.g., May, 1973). However, both connectance ($F = 13.76, df = 1,49, P < 0.05$, $r^2 = 0.34$) and average interaction strength ($F = 13.20, df = 1,49, P < 0.05$, $r^2 = 0.34$) increased as overall environmental stability decreased (Fig. 9.3), al-

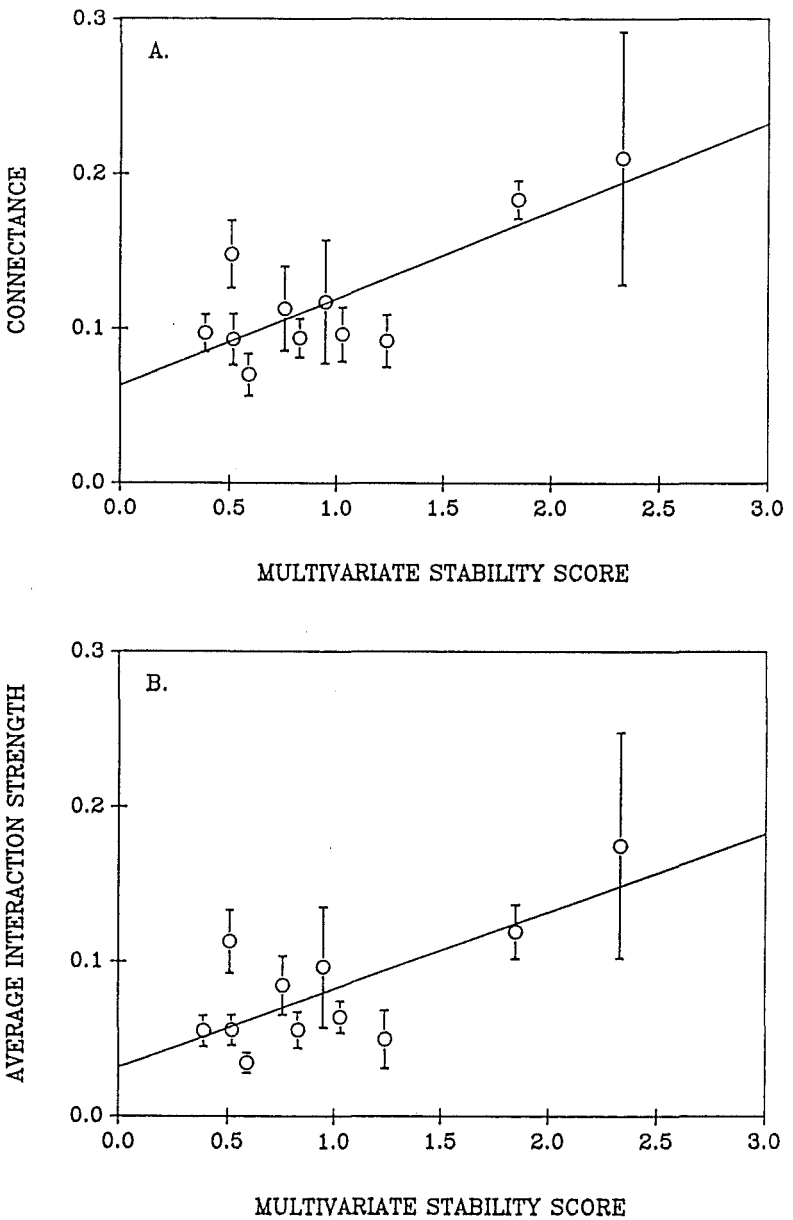


Figure 9.3. Mean connectance (A) and average interaction strength (B) as a function of overall environmental stability. Plotted values are averages of the seasonal means ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equations: connectance = 0.12 + 0.06(environmental stability score), $r^2 = 0.34$ and average interaction strength = 0.08 + 0.05(environmental stability score), $r^2 = 0.34$.

though the relationship was not constant across the seasons for either variable (F = 4.40 for connectance and F = 3.33 for average interaction strength respectively, df = 1,49, $P < 0.05$).

Nevertheless, the number of species in these communities decreased as environmental stability decreased (Chapter 5) and it may be that while connectance and interaction strength increase there is a corresponding decrease in the number of species. If so, connectance and/or average interaction strength would be expected to decrease as the number of species increases. This was indeed the case, both connectance (F = 8.01, df = 1,53, $P < 0.05$, r^2 = 0.13) and average interaction strength (F = 11.80, df = 1,53, $P < 0.05$, r^2 = 0.18) decreasing as species number increased (Fig. 9.4).

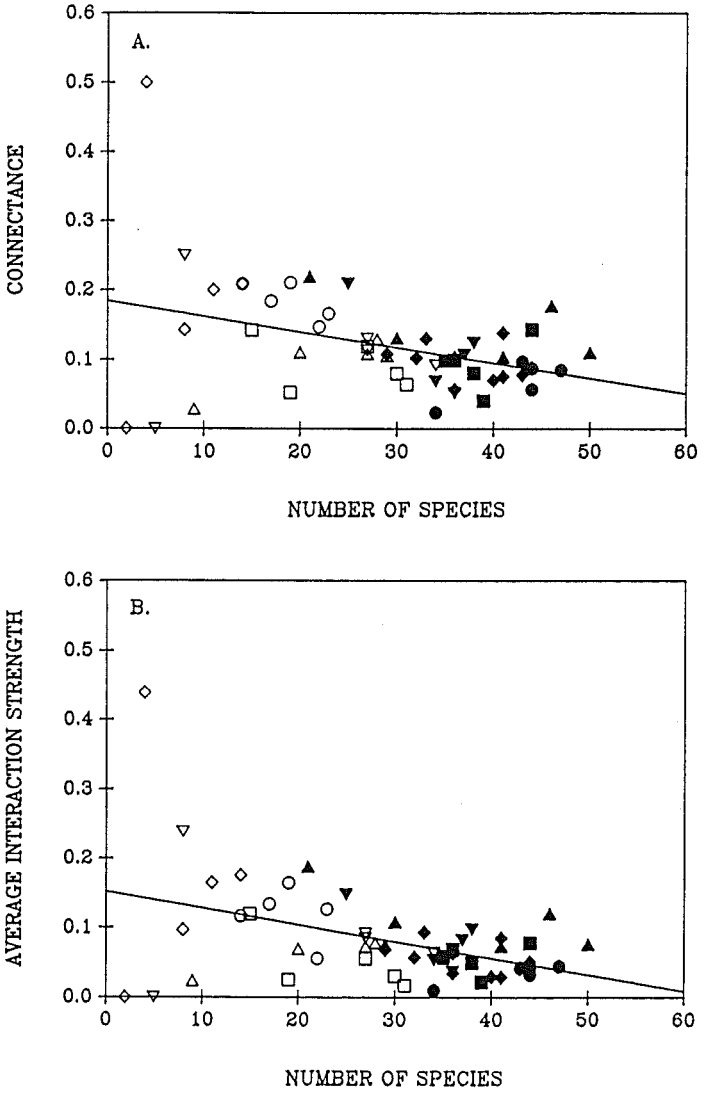


Figure 9.4. Connectance (A) and average interaction strength (B) as a function of species number. Regression analysis yielded the equations: connectance = 0.18 - 0.002(species number), r^2 = 0.13 and average interaction strength = 0.15 - 0.002(species number), r^2 = 0.18. Stable sites have solid symbols: Porter River (●), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆), Slip Spring (◆) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

How then do these aspects of complexity relate directly to resilience? Both connectance and average interaction strength were unrelated to resilience measures based on either differential (F = 0.00 and F = 0.10, df = 1,53, P > 0.05) or difference equation (F = 0.03 and F = 0.46, df = 1,53, P > 0.05) criteria (Fig. 9.5).

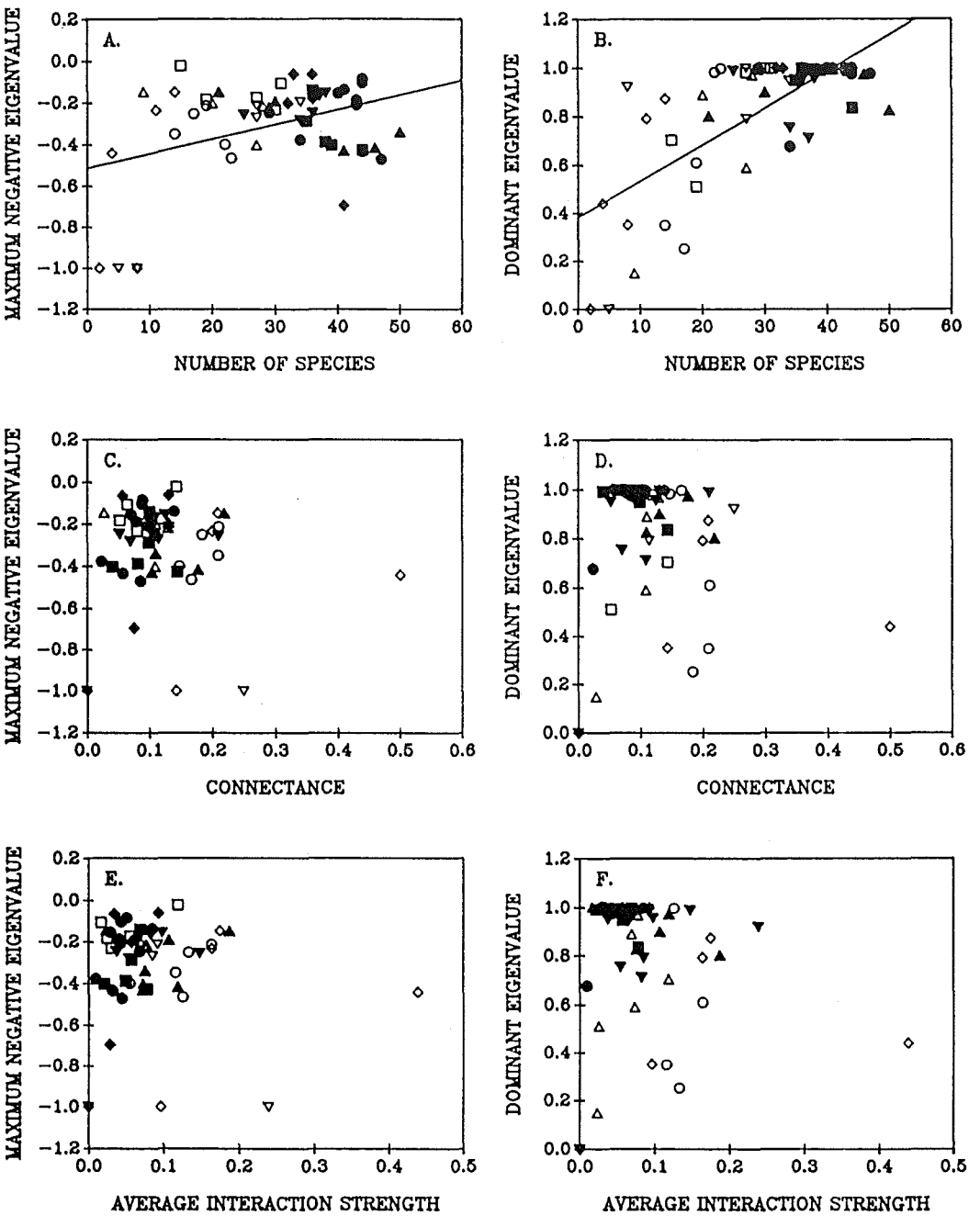


Figure 9.5. Maximum eigenvalue (A, C & E) (ignoring all positive eigenvalues) and dominant eigenvalue (B, D & F) (ignoring all those equal to or greater than one) as a function of species number (A & B), connectance (C & D) and average interaction strength (E & F). Stable sites have solid symbols: Porter River (●), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆), Slip Spring (●) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇). Only the regressions against species number were significant, yielding the equations: maximum eigenvalue = 0.007(species number) - 0.51, r^2 = 0.14 and dominant eigenvalue = 0.38 + 0.02(species number), r^2 = 0.49.

However both differential ($F = 8.65, df = 1,53, P < 0.05, r^2 = 0.14$) and difference equation ($F = 51.51, df = 1,53, P < 0.05, r^2 = 0.49$) resilience measures increased as species number increased (Fig. 9.5). That is, as the number of species increased, community resilience decreased. However, it must be remembered that these resilience measures ignore eigenvalues that fall outside the stability envelope, and in both plots the eigenvalues indicating resilience approach these stability limits very closely (zero and one for the differential and difference equations, respectively) as species number increases.

DISCUSSION

In other studies in which species associations have been investigated at the community level (Reice, 1981, 1983; Peckarsky, 1986; Lake *et al.*, 1988) a preponderance of positive associations have been taken to indicate a lack of biotic interaction (i.e., species are simply utilising common resources without competing). In these studies, either correlation techniques (as in my study) or presence/absence association measures have been used, although it is unclear whether double-negative associations were removed prior to the analysis, even though in general only the most common animals were considered. Inclusion of double-negative associations can lead to errors in interpretation (Legendre & Legendre, 1983; Ludwig & Reynolds, 1988) and when my analysis was done without removing double-negatives I found all significant correlations were positive.

The fact that several of the more stable sites had considerably more positive correlations than the unstable sites seems at first glance to be contradictory to classical ideas on biotic interactions which are considered to be stronger in more stable environments (e.g., Peckarsky, 1983). However, these stable sites also appeared to have a larger resource base (i.e., both epilithic carbon and periphyton levels were considerably higher (Chapter 3)). There may therefore be less chance of some resources, such as food, reaching a limiting level in these streams, particularly if other factors such as predation are maintaining levels at or below the carrying capacity. At the stable sites where levels of these resources were lower (e.g., Cora Lynn and Middle Bush Stream) there were in fact, many more negative than positive associations.

It is also interesting to note that most of the significant associations between predators and their prey were positive. This conforms with the predictions of classical optimal foraging theory (Krebs, 1978), that predators should be found in areas of high prey density. However, it contrasts with the findings of Malmqvist & Sjostrom (1984), Walde & Davies (1984) and Peckarsky (1988) for Northern

Hemisphere streams, although the former did find positive associations between sessile prey (such as simuliids and hydropsychids) and their predators.

The fact that the majority of the community matrices were outside the limits for local stability is also somewhat perplexing because it implies that the slightest disturbance should plummet all communities to extinction! It may be that constructing a community matrix by measuring interactions (the elements of the matrix) using spatial overlap measures is not the most appropriate approach to take. However, Seifert & Seifert (1976) constructed their matrices of *Heliconia* bract communities by manipulative examination of all possible species interactions (the most appropriate technique for constructing community matrices) and found they too were locally unstable.

There seem to be two likely possibilities as to why stream invertebrate communities persist in time despite an inherent instability in their structure. It may be that the very open nature of the communities (i.e., invertebrates are continually drifting in and out) means that stability at any given point in time is not necessary. The continual turnover of animals may in itself place stability constraints on a system that if isolated would quickly become unstable and consequently go extinct. This appears to be an area of theoretical ecology that needs further investigation, given that the generality of inherently stable (closed) communities is open to question (e.g., Seifert & Seifert, 1976).

The other possibility, that has received considerable attention in the theoretical literature, is the idea that communities are composed of compartments. A number of modelling studies (e.g., May, 1972; Goh, 1979; but see Pimm, 1979b) have shown that communities are more stable if they are organised into compartments, within which interactions are strong but between which interactions are weak. The idea that stream habitats are composed of patches is gaining increasing popularity (Pringle *et al.*, 1988; Frid & Townsend, 1989; Townsend, 1989) and my own observations of stream habitats support this view. It may be that I have considered stability at the wrong scale and that whereas overall communities may be unstable they are structured into compartments (perhaps within patches) which are themselves stable.

Given that my stream communities are inherently unstable (by local stability criteria anyway), strictly speaking it would not seem valid to compare their resilience characteristics. However, it is interesting to note that the communities in the more unstable streams (those predicted to have the greatest resilience) had eigenvalues closer to the criterion for stability, and that there did in fact seem to be increasing community resilience as the stability of the habitat decreased.

It is also worth noting that two of the components of complexity (connectance

and average interaction strength) showed no relationship to resilience, but increased as environmental stability decreased. This is contrary to the findings of Briand (1983) and Cohen *et al.* (1985) who both found connectance decreased as environmental stability decreased. However, May (1972, 1973) showed that stability could be maintained if $i(SC)^{1/2} < 1$, and therefore if i (average interaction strength) and C (connectance) both increase, the number of species (S) must show a proportionate decrease for stability to be maintained. This did indeed appear to happen in my study. A number of other workers have also found that connectance decreases with species number (e.g., McNaughton, 1978; Rejmanek & Stary, 1979; Yodzis, 1980; Pimm, 1982; Briand, 1983; Cohen *et al.*, 1985). Bruns & Minshall (1983) showed that average interaction strength in lotic predator communities decreased with species richness, although they (Bruns *et al.*, 1982) also found that filter feeders and grazers showed an increase in both these variables with increasing species richness. The finding of a decrease in resilience with an increase in the number of species in a community is also consistent with results reported by Lawlor (1980a), Bruns *et al.* (1982) and Bruns & Minshall (1983). In summary, I conclude that if my stream communities are structured in any way to maintain stability, it is by a reduction in the number of species and not by weaker or fewer interactions.

CHAPTER 10

AN EXPERIMENTAL TEST FOR COMPETITION

INTRODUCTION

In the last chapter I examined the stability of community matrices constructed on the basis of spatial overlap. The elements of these matrices should be measures of the size and sign of interaction between each species in the community with every other species (i.e., the effect of that species on all others in the community) and I used a measure of spatial resource overlap as an estimate of these interaction terms. However, the link between resource overlap and the nature of the interaction between two species is a tenuous one at best, and unless the communities are very small, performing the large number of manipulative experiments necessary to measure all interactions accurately, is impractical.

Even though it may have been impractical to examine the nature of all the interactions occurring in my study communities, it seemed worthwhile to investigate at least some of them. This was especially so, as there has been little experimental work carried out on the nature of competition in New Zealand stream invertebrate communities. Although there has been extensive work carried out overseas (e.g., McAuliffe, 1984a, 1984b; Hart 1985; Hawkins & Furnish, 1987; Hemphill, 1988; Dudley *et al.*, 1990).

I decided to examine the interaction between the snail *Potamopyrgus antipodarum* and other members of the community. This animal was chosen for a number of reasons including the fact that *P. antipodarum* was a numerically dominant member of a number of my study communities, it appeared to be easy to exclude from study patches, it has been shown to depress periphyton (resource) levels (Winterbourn & Fegley, 1989; Winterbourn, 1990) and the nature of its body form and behaviour suggested it was likely to interfere and therefore potentially compete with other species.

Competition between invertebrates may be either exploitative (i.e., there is competition for a limiting resource) or interference (i.e., the activities of one species may inhibit another without them actually sharing a common limiting resource) (Hart, 1983) and I designed the experiment to examine both these components of competition.

MATERIALS AND METHODS

The experiment was conducted at four sites: Slip Spring, Porter River (slightly

upstream from the original study site), Cora Lynn Stream and Grasmere Stream between 23 June and 4 August, 1989. Depth, current speed and temperature range recorded at these sites during the experiment are given in Table 10.1.

The unglazed lower surface of 116.6 cm^2 bathroom tiles were used as experimental substrata. These had been used successfully for previous experiments on periphyton grazing (e.g., Winterbourn & Fegley, 1989), and the algal assemblages that develop on them appear to be very similar to those on natural stream substrata. The tiles were either raised above the substrate (10-15 cm) on tent pegs, to exclude *P. antipodarum*, or placed on the stream bed where *P. antipodarum* had easy access to them. After six weeks, half of the lowered tiles were raised (any *P. antipodarum* present were removed) and half of the raised tiles were lowered. All tiles were collected three days later (long enough for any effects of interference competition to manifest, but not long enough for resource levels to become depressed), preserved in 10% formalin and all animal colonists were sorted in the laboratory as described earlier (Chapter 4).

The four experimental treatments provided different combinations of resource levels and the presence of *P. antipodarum* to test for both exploitative and interference competition. They were A) no resource depression (i.e., exploitative competition) or interference competition (raised tiles), B) resource depression and interference competition (lowered tiles), C) resource depression without interference competition (raised tiles that were initially lowered) and D) interference competition, but no resource depression (lowered tiles that were initially raised).

Five replicate tiles for each of the four treatments were placed in groups of

Table 10.1. Mean current velocity, depth and temperature (with ranges in parentheses) at Slip Spring, Porter River, Cora Lynn Stream and Grasmere Stream between 23 June and 4 August, 1989. Measurements were taken at each visit to the sites (i.e., 23 June, 2 & 4 August 1989). Current velocity was measured 10 cm from the stream bed at the centre of the channel with a Pygmy Gurley current meter and depth measured alongside each group of four tiles.

Site	Temperature °C	Depth cm	Current velocity cm s^{-1}
Slip Spring	8.6 (8-9)	13 (7-22)	57 (56-59)
Porter River	8.5 (8-8.7)	9 (6-12)	53 (49-61)
Cora Lynn Stream	9 (6-11)	10 (5-16)	38 (29-42)
Grasmere Stream	6.8 (2-10)	12 (7-21)	95 (84-103)

four (one from each treatment) at random points along a 15 m stretch of each stream. Ten smaller tiles (6 cm^2) were also placed on the lowered and raised tiles at random points along the stream. These were collected and returned to the laboratory to confirm that the grazing activities of *P. antipodarum* did depress resource levels (i.e., periphyton biomass). Periphyton biomass was determined as described in Chapter 3.

ANALYSIS

Treatment effects were examined with the GLM two way analysis of variance procedure of SAS (1985). Data were log (x+1) transformed (except periphyton biomass which was square root (x+0.5) transformed) to reduce variance heterogeneity between treatments. Multivariate community structure was examined using the detrended correspondence analysis (DECORANA) procedure of the PC-ORD multivariate package (McCune, 1987).

RESULTS

Evaluation of the treatment effects was confounded by two factors. Firstly, different responses were obtained to each of the treatments in different streams, a finding that was not altogether surprising given that each of the streams had very different densities of *P. antipodarum*. Secondly, different responses were obtained within streams depending on just where the tiles were placed. This appeared to be related to the amount of very fine sediment that accumulated on tile surfaces at some locations in the stream, probably as a result of local differences in flow. The effect of the sediment deposition was two-fold, first, it reduced periphyton biomass on the tiles, and second (probably as a consequence of the reduced periphyton levels) *P. antipodarum* densities on the unraised tiles were lowered.

Consequently, correspondence analysis (Fig. 10.1) grouped the tiles together predominantly on the basis of their positions within a stream rather than according to treatment effects. In Slip Spring, however, all raised tiles (i.e., treatment A) were grouped together (all had low scores on axis one), although three other tiles from two other treatments were also grouped with them. This was the site least affected by differential deposition of fine organic sediments.

Despite large within-site differences, the exclusion of *P. antipodarum* (and possibly other non-swimming grazers such as larvae of the caddisflies *Pycnocentrodes* and *Pycnocentria evecta*) resulted in significantly increased algal biomass (Fig. 10.2) on raised tiles ($F = 23.35$, $df = 1,30$, $P < 0.05$), the extent of which differed between sites ($F = 3.87$, $df = 3,30$, $P < 0.05$).

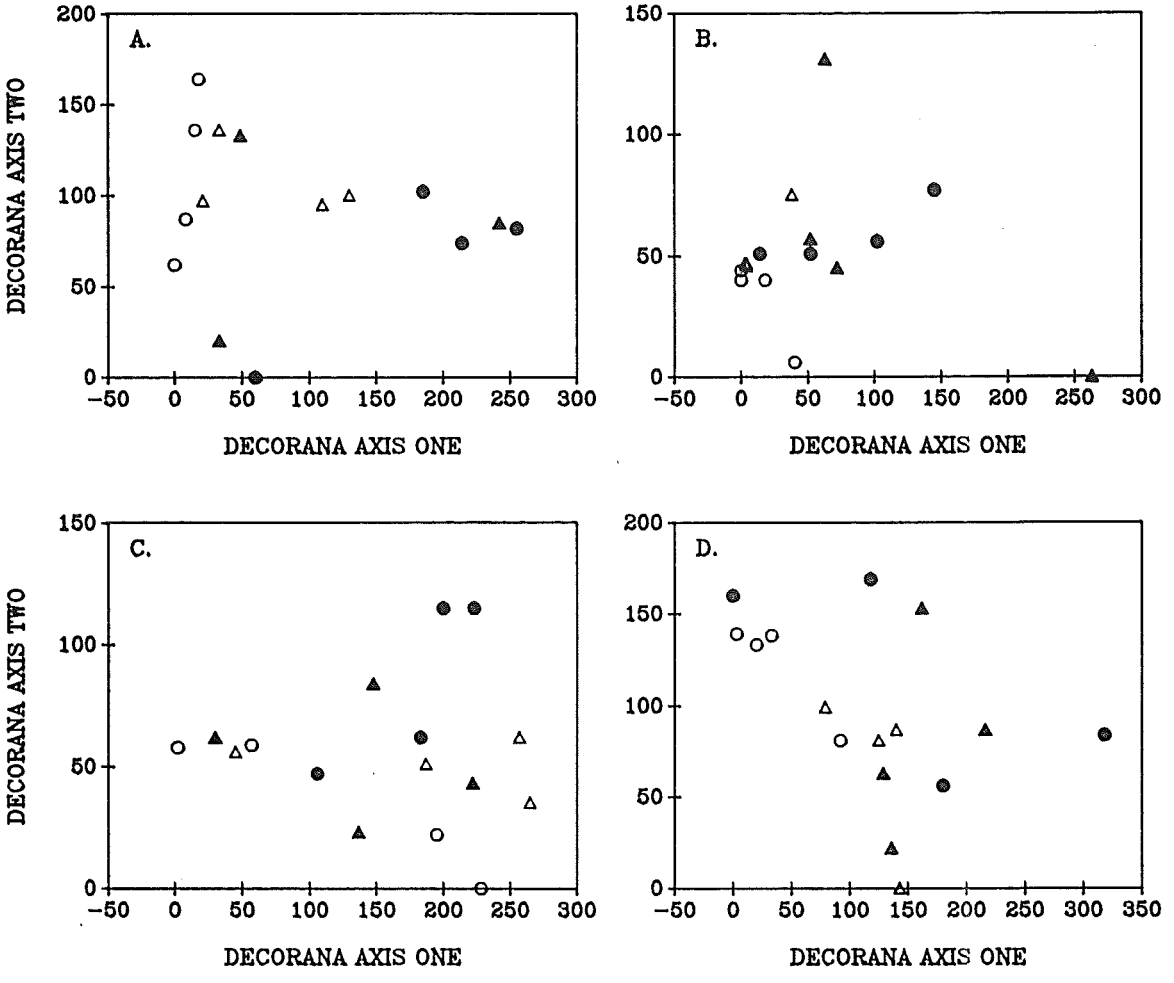


Figure 10.1. Plot of DECORANA axis one against axis two for invertebrate communities on tiles at Slip Spring (A), Porter River (B), Cora Lynn Stream (C) and Grasmere Stream (D). Tile treatments were raised (o), lowered (●), lowered and then raised (△) and, raised and then lowered (▲).

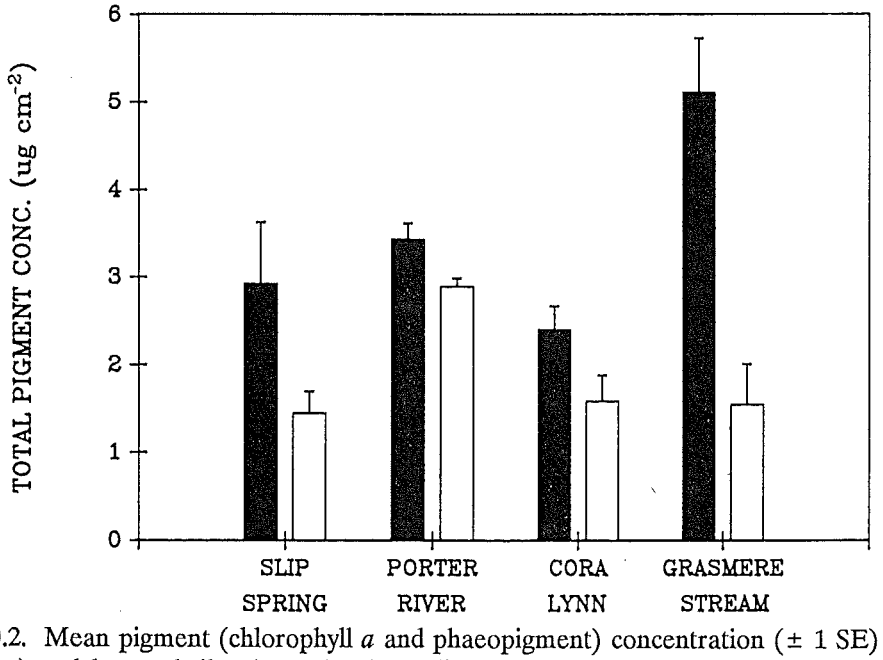


Figure 10.2. Mean pigment (chlorophyll *a* and phaeopigment) concentration (± 1 SE) on raised (filled bars) and lowered tiles (open bars) at Slip Spring, Porter River, Cora Lynn Stream and Grasmere Stream.

Total numbers of invertebrates present on the tiles (Fig. 10.3) also differed significantly between treatments (F = 3.12, df = 3,57, P < 0.05), and although responses to each of these treatments appeared to differ among the sites this was not statistically significant (F = 1.78, df = 9,57, P > 0.05). However, except in Grasmere Stream, highest densities occurred on the raised tiles (i.e., treatment A). Numbers of colonising taxa (Fig. 10.4) were not significantly different among

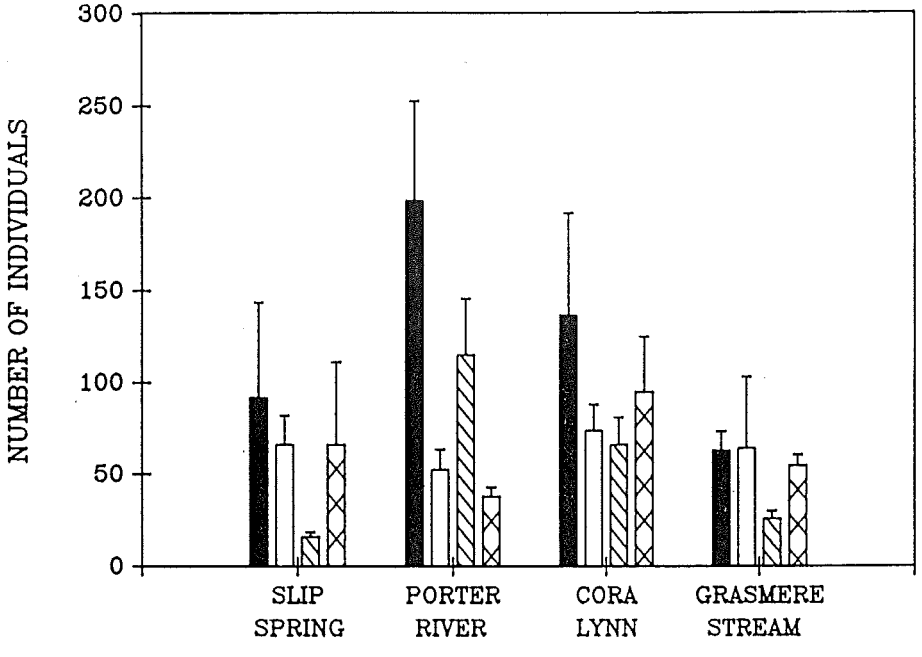


Figure 10.3. Mean number of invertebrates (± 1 SE) collected on raised (filled bars), lowered (open bars), lowered then raised (diagonally shaded bars) and raised then lowered tiles (cross-hatched bars) at Slip Spring, Porter River, Cora Lynn Stream and Grasmere Stream.

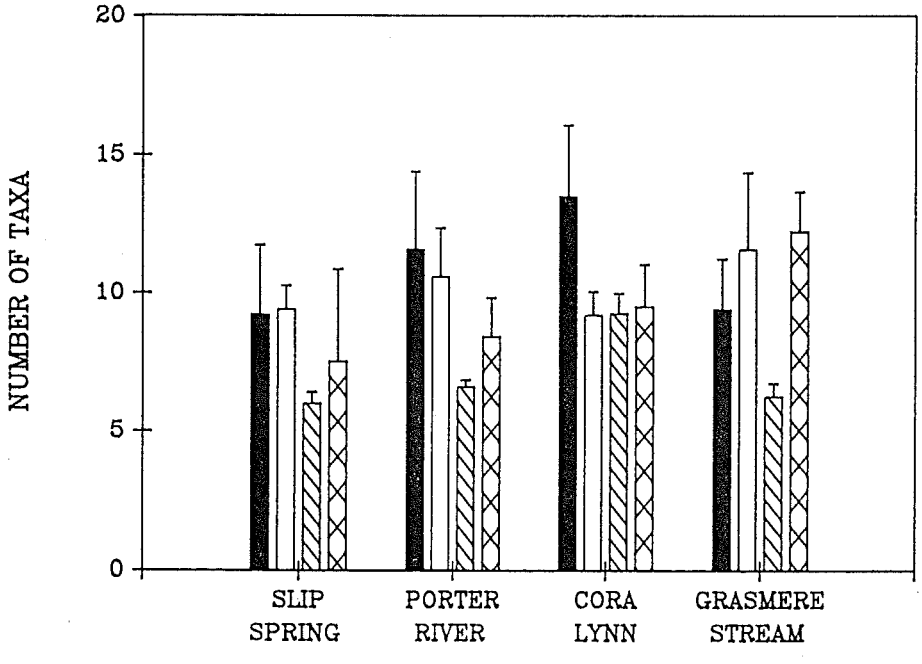


Figure 10.4. Mean number of taxa (± 1 SE) collected on raised (filled bars), lowered (open bars), lowered then raised (diagonally shaded bars) and raised then lowered tiles (cross-hatched bars) at Slip Spring, Porter River, Cora Lynn Stream and Grasmere Stream.

treatments (F = 2.63, df = 3,57, P > 0.05), although in both Porter River and Cora Lynn the highest number of taxa were on the raised tiles (i.e., treatment A).

The density of Simuliidae on the tiles (Fig. 10.5) was significantly different

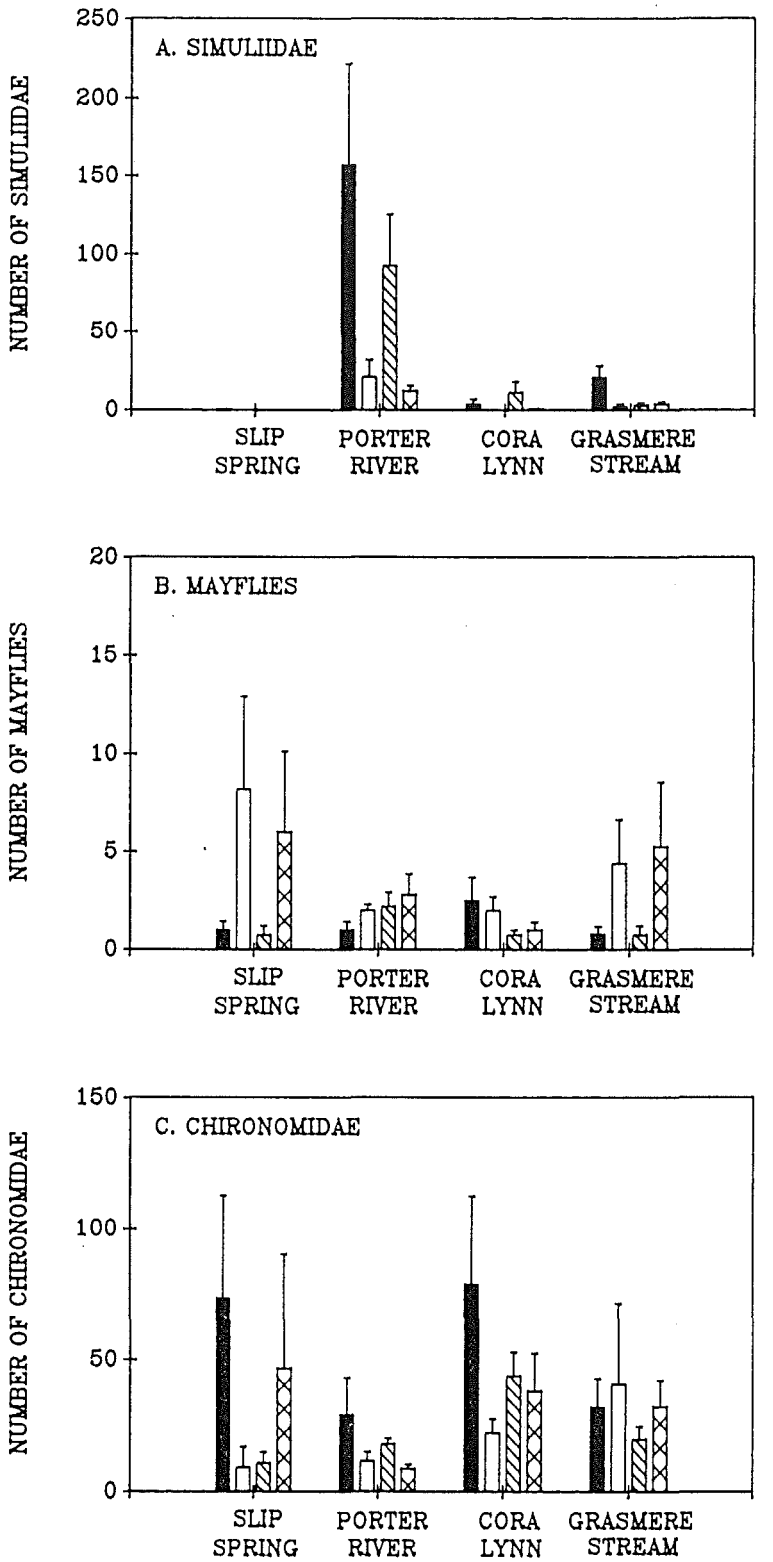


Figure 10.5. Mean number of Simuliidae (A), mayflies (B) and Chironomidae (C) (± 1 SE) on raised (filled bars), lowered (open bars), lowered then raised (diagonally shaded bars) and raised then lowered tiles (cross-hatched bars) at Slip Spring, Porter River, Cora Lynn Stream and Grasmere Stream.

between treatments ($F = 3.37, df = 3,43, P < 0.05$), and was most pronounced at the Porter River site where densities were considerably higher on raised tiles (A & C) than on lowered tiles (B & D). Mayfly densities (all *Deleatidium* sp. except at Grasmere Stream where *Nesameletus* sp. was also included) (Fig. 10.5) were also significantly different between treatments ($F = 3.38, df = 3,57, P < 0.05$), however, they were highest on lowered tiles (B & D), except at Cora Lynn. The lowered tile treatment (B) was significantly different from both the raised tile treatments (A & C), but was not significantly different from treatment D (raised then lowered tiles), while these three treatments (A, C & D) were not different from each other. The other common taxon, the family Chironomidae (species lumped together for the analysis) also exhibited significantly different densities among treatments ($F = 3.34, df = 3,57, P < 0.05$), but only raised (A) and lowered (B) tiles were significantly different from each other.

DISCUSSION

The results of this experiment are rather equivocal because of differences in treatment effects both within and between streams. However, the results indicate that *P. antipodarum* (and possibly other grazers) were reducing periphyton biomass in these streams as has been reported previously for Slip Spring (Winterbourn & Fegley, 1989) and other Canterbury streams (M.J. Winterbourn, unpublished data). Given that *P. antipodarum* is reducing resources, there must be potential at least for competitive interactions between it and other invertebrates dependent on the same periphyton resources.

Total numbers of invertebrates and taxa were generally higher on raised tiles (i.e., treatment A) than on those for other treatments, suggesting that if competition is having an effect, it is through both interference and exploitative competition by those invertebrates excluded from the tiles (primarily *P. antipodarum*). The exact nature of the relationship and its strength seems to depend on both the site and taxa involved.

The common taxa whose densities on tiles were examined, also exhibited different responses to the treatments in different streams, particularly with respect to treatments C and D (the tiles designed to differentiate between exploitative and interference competition). However, all but one of the significant differences recorded were between the raised (A) and lowered (B) treatments (neither being significantly different from either treatments C or D) and if these latter two treatments are ignored, responses are remarkably consistent across all the sites. The Chironomidae and Simuliidae both had higher population densities on the raised

(A) than on the lowered (B) tiles. It is unclear just what form of competition could have led to the differences in chironomid densities (responses to treatments C and D differed in each of the streams), but the higher densities of simuliids on treatment C (lowered then raised) than on any of the lowered tiles (B & D), although not significant, suggests that interference competition may have been involved. However, observation of interactions between *P. antipodarum* and simuliids in a laboratory stream did not provide support for this idea, and it is likely that simuliid larvae preferred the raised tiles simply because they facilitated feeding. Why mayflies had significantly higher densities on lowered (B) than on raised tiles (A) is also unclear. They may prefer lower biomass epilithon which is more readily removed and ingested by their primarily brushing mouth parts (as found by Scrimgeour *et al.* (1991) for a Canadian stream), but such an explanation does not explain the high densities found on treatment D tiles that had well developed periphyton. It seems more likely that the lowered tiles are preferred because they offer more cover for the mayflies which are strongly negatively phototactic.

In summary, it is difficult to come to any firm conclusions about the effect of *P. antipodarum* on other invertebrate species in these communities because of the large differences in treatment responses found both within and between streams. However, the periphyton grazing by the snails did lead to reduced resource levels, and this offers the potential for competitive interactions. My data suggests that such interactions may be occurring, but does no more than suggest this.

CHAPTER 11

OVERLAP OF SPATIAL RESOURCE UTILIZATION

INTRODUCTION

The importance of resource partitioning amongst closely related species as a force in structuring communities has been an area of interest in ecology since it was introduced early this century by Elton (1927), Grinnell (1917, 1924, 1928) and others (for an historical review of its development see Schoener, 1989). The term "ecological niche" is often used to describe the resource usage of a particular species, although the definition of the term "niche" is often very vague (Pianka, 1981) and it may prove impossible to measure (Pianka, 1975). Associated with this interest in resource partitioning has been a vast body of theoretical work (for reviews see Abrams, 1983; Giller, 1984; Schoener, 1986b, 1988, 1989) which has considered the extent to which resource use can overlap between two species without leading to competitive exclusion. Early work (MacArthur & Levins, 1967; MacArthur, 1972; May & MacArthur, 1972; May, 1973, 1974) suggested that there was a limit to how similar two species could be and still coexist, or alternatively allow the invasion and persistence of a third species (this is often described as limiting similarity). However, more recent work, both theoretical and empirical, has thrown considerable doubt on the generality and/or validity of the assumptions and conclusions associated with this early work (see Schoener, 1986b and 1989 for discussions).

Much of the early theoretical work also considered the effect of environmental variability on the question of "limiting similarity" and coexistence (MacArthur, 1972; May & MacArthur, 1972; May, 1973). It was suggested that environmental variability places constraints on the degree to which two species can overlap in resource usage, however the limit to this overlap is insensitive to the degree of environmental variability, unless this variation is "very severe". However, as for the concept of limiting similarity *per se*, more recent work (e.g., Abrams, 1976; Turelli, 1981) has thrown doubt on the early theories concerning environmental variability and resource overlap (see Abrams, 1983 for a review). The exact nature of the relationship between these two variables seems to depend on both the degree of environmental variability and the particular models invoked to explain these patterns (Schoener, 1986b).

The relationship between resource overlap and species diversity has also been an area of both theoretical and empirical interest (Pianka, 1981). MacArthur (1972) postulated that diversity could be increased in a community only if the diversity of resources in the environment increased, the range of resources used by an average species (niche breadth) decreased, or the extent of average resource overlap increased. Considerable empirical support has been forthcoming for these ideas, and the diversity of bird (MacArthur, 1972), squirrel (Emmons, 1980) and insect assemblages (Hendrix, 1980; Moran & Southwood, 1982) for example, have been found to be related to plant diversity and structure (and conceivably resource diversity). Both tropical stream fish (Zaret & Rand, 1971) and Galapagos ground finches (Smith *et al.*, 1978) exhibit decreasing niche breadth with decreasing food availability, however, Davies *et al.* (1981) found that predatory leeches increase niche breadth and overlap with increasing prey availability. Similarly, whereas lizard (Pianka, 1974, 1975), desert rodent (M'Closkey, 1978), ant (Bernstein & Gobbel, 1979) and tropical stream fish communities (Zaret & Rand, 1971) among others, exhibited decreasing niche overlap with increasing species richness, some small mammal assemblages were found to have a positive relationship between niche overlap and species diversity, although niche breadth remained invariant (Gorman, 1979; Porter & Dueser, 1982).

For such patterns to occur however, communities must be at or near equilibrium in habitats where resources are limiting, conditions that are more likely to occur in relatively stable environments (Minshall *et al.*, 1985). While species in predictable environments may be able to reduce competition by becoming more specialized, species in unpredictable environments may be unable to specialize on a specific range of resources because of the constantly changing conditions (MacArthur, 1975). Alternatively, if communities are not saturated with species (i.e., resources are not limiting) increasing species diversity will simply be associated with increasing niche overlap, and niche breadth will be unchanged.

Some evidence suggests that many stream invertebrate communities may fall into this latter category. For example, Rader & Ward (1989) found that trophic, temporal and spatial overlap of scraper/collector-gatherer guilds were not significantly different between a regulated (predictable) and unregulated (unpredictable) section of the Colorado River and Bruns *et al.* (1982) found a positive relationship between diversity and niche (body size) overlap in grazer and filter feeder guilds. Similarly, Tokeshi (1986) found that temporal and dietary overlap within epiphytic chironomid assemblages was significantly greater than that expected in a randomly constructed community and although Tokeshi & Townsend (1987) found that spatial overlap between species in these assemblages was sig-

nificantly less than that expected by chance, this was the result of the chironomids aggregating in patches, between which overlap was no less than that expected by chance. However, Bruns & Minshall (1983) and Hildrew *et al.* (1984) have both found a decrease in niche overlap with increasing species richness in lotic predator and detritivorous stonefly assemblages, respectively.

In Chapter 9 of this thesis I used spatial overlap as a rough approximation of the degree of competitive interaction between species in my study communities. However, in evaluating the statistical significance of these interactions, any non-significant association was automatically set to zero. In so doing, a very truncated distribution of the degree of spatial overlap was produced. In the present chapter I examine spatial overlap *per se* between species in my invertebrate communities, using non statistical, niche overlap techniques, and consider its relationship with environmental stability.

MATERIALS AND METHODS

Niche Overlap and Niche Breadth Measures

As with many other measures in ecology, a large number of techniques and formulae have been proposed for calculating both niche overlap and niche breadth. For reviews, see Pielou (1972), Abrams (1980), Hurlbert (1978), Lawlor (1980b) and Zaret & Smith (1984). I have used two niche overlap measures, which turned out to give very similar results.

The first of these is Schoener's (1970) niche overlap measure where

$$\text{niche overlap} = \sum \min (p_{xi}, p_{yi})$$

where p_{xi} = the proportion of species x using resource state i (stones in this case), and p_{yi} = the proportion of species y using resource state i.

This index has been advocated by a number of the above reviews as the best to use because it is simple to calculate, free of assumptions about competition, allows intercommunity comparisons and is not sensitive to the scale of resource perception.

The second measure of niche overlap I calculated was Pianka's (1973) overlap measure because it has been used in similar studies of stream invertebrate communities.

$$\text{This gives niche overlap} = \frac{\sum p_{xi} \cdot p_{yi}}{(\sum p_{xi}^2 \cdot \sum p_{yi}^2)}$$

where p_{xi} and p_{yi} are as above.

Both overlap indices give a measure in the range 0 (no overlap) to 1 (complete overlap).

Niche breadth was calculated using Levins (1968) measure.

Thus niche breadth = $\frac{1}{n. \sum p_{xi}^2}$

where n = the number of resource states and the other parameters are as above.

Niche overlap measures were calculated for every pairwise combination of species (niche breadth for all species) in each of the communities (i.e., each seasonal sample), and the calculated variables were then averaged to give a single (average) measure for each community.

Randomized Simulation Studies

The niche overlap and breadth measurements obtained suggested that the assemblages collected on stones at some sites may have been structured purely by random colonisation processes. To test this hypothesis, I examined whether randomly accumulating more individuals could have led to the observed increase in niche overlap and whether the assemblages on these stones could have been produced by random colonisation alone. Random stone assemblages (i.e., an equivalent number of individuals to that collected on each stone) were constructed by randomly drawing individuals from the pool of individuals and taxa present at that site (i.e., the total number of individuals in each species collected on the fifteen stones). This was carried out using a Turbo BASIC program that I wrote. For the analysis of the niche overlap patterns, 35 trials were conducted at each fraction of the community (see later) and for the stone assemblage analysis 50 trials for both random/real and random/random comparisons were conducted (see later for more details).

RESULTS AND DISCUSSION

Average niche breadth and the two niche overlap measures are plotted against overall (multivariate) stability in Fig. 11.1. All three variables decreased as stability declined (F = 19.25 (r^2 = 0.48), F = 30.00 (r^2 = 0.45) and F = 25.60 (r^2 = 0.41) for niche breadth, overlap and Pianka's overlap respectively, df = 1,49 $P < 0.05$). Only niche breadth differed significantly with season (F = 6.40, df = 4,49, $P < 0.05$), but no variable exhibited differing relationships with stability (i.e., slopes) in different seasons.

This suggests increased competition pressure that might be expected to occur

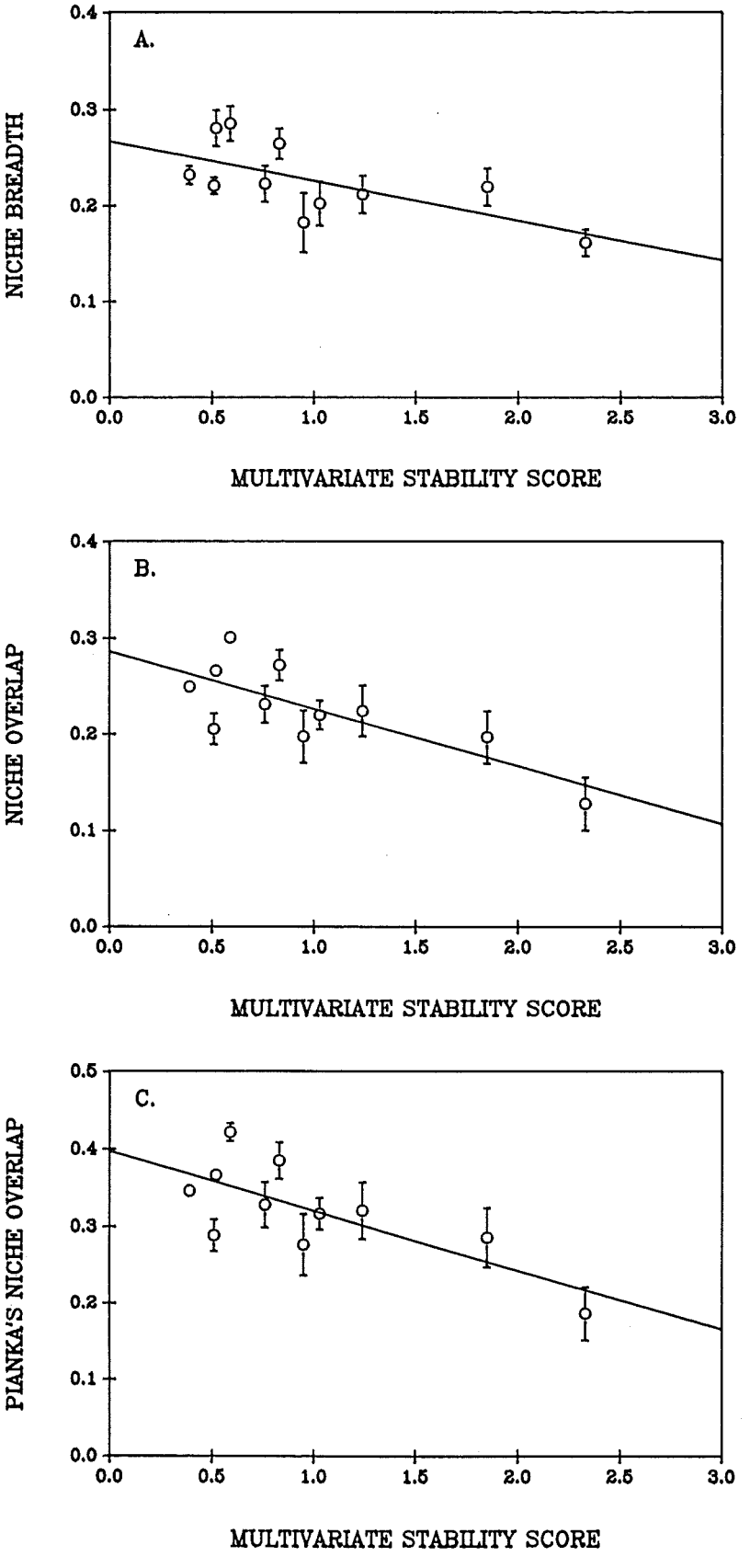


Figure 11.1. Mean niche breadth (A), niche overlap (B) and Pianka's niche overlap (C) as a function of overall stability (multivariate stability score). Plotted values are averages of seasonal means (± 1 SE). Regression analysis was performed including seasonal comparisons to yield the equations, niche breadth = 0.23 - 0.04(stability score), r^2 = 0.48, niche overlap = 0.26 - 0.06(stability score), r^2 = 0.45, Pianka's niche overlap = 0.36 - 0.08(stability score), r^2 = 0.42.

in more stable environments, was either not occurring or was not affecting niche overlap or breadth. It may be that the division of resources was occurring in guilds within the communities so that any differences in resource usage were not obvious at the community level, however as 60% - 90% of the individuals and species in these communities are in the same guild (i.e., collector/browser, see Chapter 13) this seems unlikely. Niche overlap is more likely to decrease simply because there are fewer species and/or individuals at the less stable sites, and therefore less chance of two species occurring on the same stone. Similarly, niche breadth may decrease because each species contains fewer individuals, and there are consequently fewer conspecifics available to occupy any particular stone. That the decline in niche overlap and breadth with decreasing stability may be the result of lower density and diversity at these sites is borne out by the plot of niche overlap and breadth against species number (Fig. 11.2). Both variables exhibit a significant increase with increasing number of species (F = 40.31 (r^2 = 0.43) and F = 44.20 (r^2 = 0.45) for niche overlap and breadth respectively, df = 1,53, $P < 0.05$).

It is interesting to note that in other studies that have found an increase in niche overlap with increasing species richness (e.g., Bruns *et al.*, 1982 (aquatic invertebrates); Gorman, 1979 (small mammals)), niche breadth has been found to be negatively correlated or invariant to increases in species number. Whereas, in this study there appears to be an increase in both niche breadth and niche overlap. Resource levels have also been shown to affect niche breadth and overlap (Giller, 1984), and in my streams, resources probably decreased with decreasing stability (periphyton biomass was lower and the number of stones available for colonisation (i.e., undisturbed) was probably also lower). Zaret & Rand (1971) and Smith *et al.* (1978) both reported declining niche breadth with decreasing resources, so this may also have been a factor here.

It is possible, however, that the increases in both overlap and niche breadth observed in the more stable sites were the result of more species and/or more individuals being available for colonisation of resource states (i.e., stones). To test this idea, I used data from the Porter River spring 1 sample (a site with a high diversity and density of invertebrates), randomly accumulated fractions (0.005, 0.01, 0.1, 0.2, 0.5 and 1) of the total number of invertebrates collected on each of the stones at this site and calculated niche breadth and overlap for all the species present. By this means I was able to examine how niche overlap and breadth changed as more species and individuals accumulated. A plot of niche breadth and overlap against the fraction of the community sampled is given in Fig. 11.3. As predicted, both variables increased as more individuals and species were accumulated. However, it is interesting to note that the observed values of niche over-

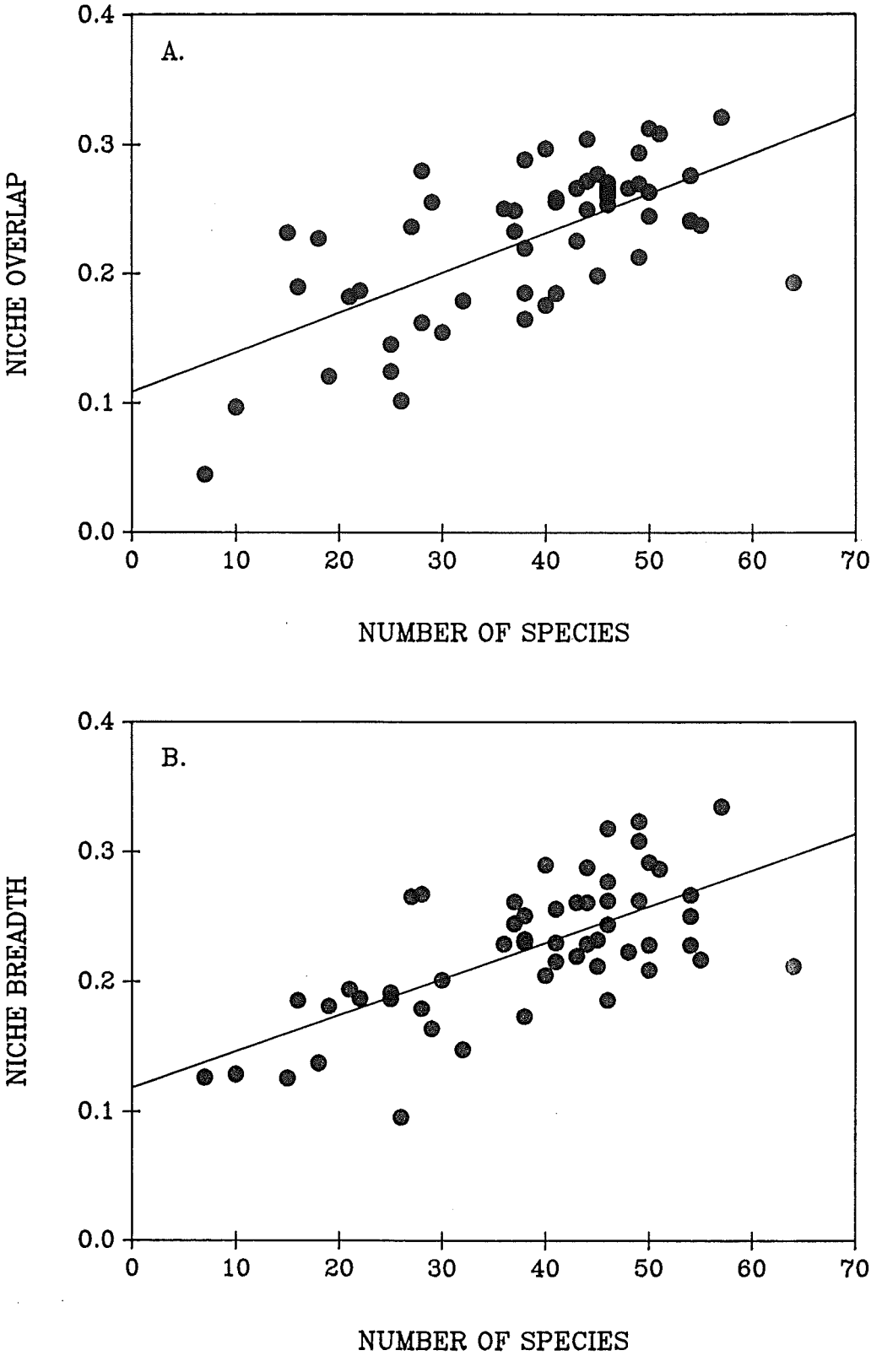


Figure 11.2. Niche overlap (A) and niche breadth (B) as a function of species number. Niche overlap = 0.11 + 0.003(species number), r^2 = 0.43 and niche breadth = 0.12 + 0.003(species number), r^2 = 0.45.

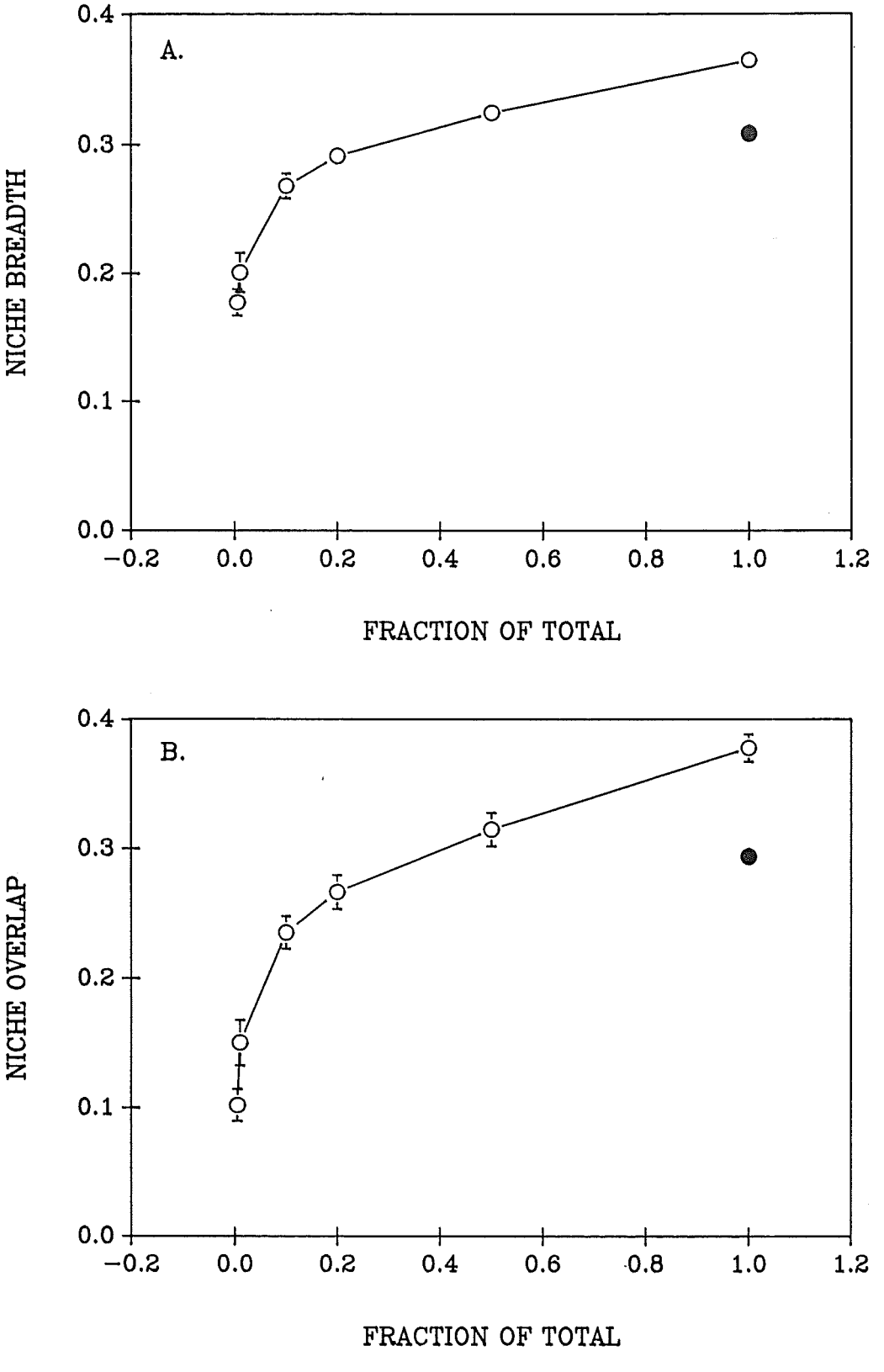


Figure 11.3. Mean niche breadth (A) and niche overlap (B) (± 99% confidence limits) calculated for randomly accumulated fractions of the Porter River spring 1 community. Filled circles show the niche parameters calculated for the community using the full field data set.

lap and breadth for the real community were lower than those predicted for a randomly accumulated community of the same size and composition. Perhaps overlap and breadth increase because of increasing resource levels (associated with increased stability) but are constrained by other abiotic or biotic influences (e.g., predation or competition) that keep niche measures below those which would be attained through simple random processes.

If biotic influences are stronger in more "benign" environments as predicted by Peckarsky (1983), then community structure at these sites would be expected to deviate more from random than those at the very unstable sites, where chance colonisation events may predominate. To test this, I randomly accumulated the same number of individuals collected on each of the stones, from a pool of potential colonists present at that site (i.e., the total number of individuals in each species collected on the fifteen stones) and measured how similar these assemblages were to the real communities using Euclidean distance. To examine whether these distances were greater than those expected by chance I also calculated the Euclidean distance between two assemblages drawn at random. This was done for the spring 1 (a season with stable conditions), summer, and winter (a season with very unstable conditions) samples, from all sites.

Results for each of the three stone size classes (large, medium and small) are given in Table 11.1. For the more stable sites, all but one size class (small at

Table 11.1. Mean, minimum and maximum Euclidean distance between random and real stone communities (Real) and two random communities (Random) for large, medium and small stone size classes. Values of T obtained in comparisons of means are also given for each size class. Significance levels are $P < 0.001$ ***, $P < 0.01$ **, $P < 0.05$ * and non significant $P > 0.05$.

		Large stones				Medium stones				Small stones			
		Min.	Mean	T value	Max.	Min.	Mean	T value	Max.	Min.	Mean	T value	Max.
UNSTABLE SITES													
Kowai River													
Spring 1	Real	6	33	(11.2)***	70	4	27	(13.0)***	54	5	19	(15.6)***	42
	Random	6	23		57	4	15		49	2	9		21
Summer	Real	2	7	(2.9)**	17	0	5	(-0.4)	12	0	5	(5.4)***	17
	Random	2	6		21	2	5		14	0	3		7
Winter	Real	2	6	(-2.3)	10	2	4	(-0.7)	8	0	1	(-0.4)	3
	Random	3	6		14	2	4		8	0	1		4
Whitewater Stream													
Spring 1	Real	8	25	(11.1)***	66	7	21	(15.7)***	56	2	11	(12.4)***	24
	Random	6	15		37	5	12		28	2	6		18
Summer	Real	5	22	(11.1)***	49	6	14	(15.5)***	27	1	6	(2.5)**	15
	Random	5	13		36	4	10		26	2	5		16
Winter	Real	11	65	(20.0)***	234	1	16	(17.8)***	50	0	2	(4.3)***	9
	Random	2	12		54	1	5		19	0	1		7

Table 11.1. (*Continued on following pages*)

Table 11.1. (*Continued*)

Dry Stream													
Spring 1	Real	10	45	(22.6)***	92	5	15	(9.7)***	30	5	17	(15.3)***	44
	Random	5	16		39	2	11		28	2	8		22
Summer	Real	24	57	(32.3)***	96	9	19	(14.3)***	34	1	7	(5.5)***	14
	Random	11	23		48	5	13		29	0	5		14
Winter	Real	6	16	(15.4)***	34	1	12	(6.0)***	46	0	3	(1.8)*	9
	Random	4	10		24	1	5		12	0	2		7
Craigieburn Cutting Stream													
Spring 1	Real	7	20	(13.9)***	34	4	9	(3.4)***	18	1	4	(0.2)	8
	Random	4	13		30	2	9		23	1	4		10
Summer	Real	3	13	(10.3)***	26	3	7	(2.1)*	12	1	5	(1.8)*	15
	Random	3	9		20	3	6		13	1	4		12
Winter	Real	0	3	(-2.1)	8	0	3	(2.6)**	5	0	0	(-0.6)	2
	Random	0	3		8	0	2		5	0	0		2
Bruce Stream													
Spring 1	Real	2	6	(6.2)***	11	0	7	(5.5)***	20	0	1	(0.7)	3
	Random	2	5		14	0	5		14	0	1		3
Summer	Real	1	5	(4.0)***	17	1	4	(0.0)	10	0	2	(2.0)*	5
	Random	2	4		9	0	4		9	0	2		5
Winter	Real	0	1	(-3.0)	4	0	1	(1.3)	2	0	0	(0.1)	1
	Random	0	1		3	0	1		3	0	0		1
STABLE SITES Porter River													
Spring 1	Real	60	143	(46.9)***	297	27	84	(28.9)***	190	12	34	(25.6)***	70
	Random	11	31		73	9	24		44	3	12		32
Summer	Real	26	192	(19.8)***	554	28	107	(30.5)***	207	32	50	(49.0)***	82
	Random	15	38		100	11	31		86	5	15		34
Winter	Real	22	79	(19.2)***	200	13	30	(20.5)***	56	7	22	(14.4)***	55
	Random	14	29		57	7	16		33	3	12		26
Slip Spring													
Spring 1	Real	21	87	(33.3)***	167	12	49	(24.6)***	90	2	23	(13.5)***	53
	Random	8	24		74	4	17		58	2	11		39
Summer	Real	187	371	(61.0)***	615	43	159	(33.4)***	338	48	94	(53.9)***	149
	Random	16	48		135	15	32		82	9	23		58
Winter	Real	44	333	(25.5)***	695	23	91	(24.2)***	226	9	67	(16.8)***	148
	Random	7	46		120	9	27		86	5	18		53
Cora Lynn Stream													
Spring 1	Real	30	95	(34.0)***	180	18	33	(23.9)***	75	2	17	(13.3)***	35
	Random	11	25		49	6	17		37	2	8		21
Summer	Real	14	61	(21.7)***	135	3	40	(9.8)***	115	3	19	(13.6)***	51
	Random	7	20		47	2	16		41	2	8		21
Winter	Real	6	13	(7.1)***	25	3	12	(7.2)***	27	2	5	(3.9)***	10
	Random	5	11		22	2	9		26	2	4		8

Table 11.1. (*Continued*)

Middle Bush Stream													
Spring 1	Real	7	25	(13.8)***	51	8	19	(11.5)***	39	2	8	(8.8)***	23
	Random	7	15		31	7	13		29	2	5		12
Summer	Real	11	22	(16.7)***	45	2	16	(5.1)***	34	0	4	(2.3)*	10
	Random	7	14		22	3	11		23	0	4		8
Winter	Real	6	14	(4.0)***	28	4	11	(7.3)***	26	0	3	(0.7)	7
	Random	5	12		24	3	8		20	0	3		6
Grasmere Stream													
Spring 1	Real	30	57	(32.3)***	108	16	32	(25.8)***	62	4	17	(12.0)***	46
	Random	9	23		64	7	16		32	3	9		22
Summer	Real	43	107	(27.2)***	204	29	84	(27.7)***	194	10	26	(19.0)***	54
	Random	18	41		120	12	30		87	3	14		31
Winter	Real	21	57	(19.9)***	134	12	26	(22.3)***	44	0	9	(4.2)***	24
	Random	8	25		61	8	16		33	0	7		20
Lake Grasmere													
Spring 1	Real	59	180	(30.0)***	491	25	120	(27.8)***	312	5	42	(9.6)***	180
	Random	7	35		108	7	25		69	2	11		59
Summer	Real	98	241	(42.7)***	492	36	101	(40.1)***	159	26	71	(42.2)***	101
	Random	12	42		108	13	32		66	9	22		45
Winter	Real	121	198	(71.2)***	287	14	65	(18.3)***	183	8	36	(28.1)***	64
	Random	12	30		95	5	20		51	3	12		30

Middle Bush) had a larger difference between real and random communities than between two randomly drawn communities. That is, the communities actually present on the stones appear to be significantly different from those expected to accumulate by chance. At the unstable sites the extent of the difference between random and real communities depended on both the season and stone size. Thus, real communities were different from those drawn randomly in the seasons with more stable conditions (spring 1 and summer) and for the larger (more stable) stones. In contrast, actual assemblages on medium and small stones at several of the unstable sites did not differ from those that would accumulate by chance.

In summary, it appears that communities at stable sites (and on more stable substrates) differ from those that would be expected to accumulate by chance, however the mechanism of these differences is still unclear.

CHAPTER 12

AN EXPERIMENTAL STUDY OF THE EFFECT OF PATCH DISTURBANCE ON INVERTEBRATE COMMUNITY STRUCTURE

INTRODUCTION

One of the principal aims of this study was to establish whether or not a relationship exists between community stability and environmental stability, and in particular whether certain characteristics of some communities (such as their complexity) enable them to survive in the face of continual disturbance. Although environmental stability has always been considered an important structuring force in stream invertebrate communities (Power *et al.*, 1988; Resh *et al.*, 1988) there appears to have been little consideration of whether communities in streams with more severe disturbance regimes have more or less complex communities, and whether community complexity in turn affects their stability (i.e., ability to recover from a disturbance). A number of experimental studies have been carried out to examine the effects of disturbance on stream invertebrate communities (e.g., Clifford, 1982; Reice, 1984, 1985; Robinson & Minshall, 1986; Doeg *et al.*, 1989; Lake *et al.*, 1989), however, I am only aware of one study (Malmqvist & Otto, 1987) that has examined the response of more than one stream community, and even then there was little attempt to relate the observed responses to differences in the environmental conditions at each of the sites.

This seems to be in stark contrast to other areas of ecology, especially theoretical ecology, where the relationship between the complexity of a community and its ability to cope with disturbances has been a dominant theme of research since the 1950s (May, 1981; Pimm, 1982; Kikkawa, 1986; McNaughton, 1988; Walker, 1989). It was initially suggested that more complex communities would be more stable (Elton, 1958; MacArthur, 1955) however, as a result of the mathematical modelling approaches of the 1970s (for a review see May, 1981), more complex communities are now generally held to be less stable.

Most of these mathematical studies have been based on models of Liapunov functions which relate to the local stability of matrices. Local stability (i.e., the ability to recover from a small disturbance) can be assessed by examining the eigenvalues of a matrix which describes a particular system (for more details see Chapter 9). In Chapter 9 I used these techniques to evaluate (local) stability of community matrices that I constructed for my study communities, and found that all communities had eigenvalues outside the constraints for a stable matrix. However, matrices for communities at less stable sites did have eigenvalues closer to the stability criteria, and if the eigenvalues that lay outside the boundaries denoting stability were ignored, also had eigenvalues that suggested these communities would be more resilient to disturbance (i.e., they would return to pre-disturbance levels more quickly).

However, whereas mathematical studies allow stability to be defined simply and precisely it is less easy to define for real communities. Local and global stability may be useful concepts when defined mathematically, but how do they relate to the real world? Is a small disturbance the arrival of a new species on a stone, the movement of a stone or a small increase in discharge, and if so when does a small disturbance become a large disturbance? Examining constraints for global stability (i.e., recovery from large disturbances) may in fact change the conditions necessary for a community to be stable (Pimm, 1979a). In different systems, a given disturbance may also be perceived in different ways; for example a light shower of rain is likely to have little impact on a stream community, but it may represent a large disturbance to the microbial community on the surface of a decomposing leaf. There are also inherent difficulties in constructing community matrices in the first place, unless the study communities are very small (for a discussion see Chapter 9).

Despite all these difficulties, a number of researchers (e.g., Seifert & Seifert, 1976; Lawlor, 1980a; Bruns *et al.*, 1982; Bruns & Minshall, 1983; Levitan, 1987) have assessed the local stability of a community by examining the eigenvalues of its community matrix. But, there does not appear to have been any attempt to relate the eigenvalues of a community matrix to the response of that community to a real disturbance.

In this chapter, I examine the results of different degrees of experimental disturbance on patches of substrate in four of my study streams (two environmentally stable and two unstable). I did this firstly, to test whether the patterns in community structure discussed in the previous chapters were, as suggested, related to differences in the environmental stability of the sites. By manipulating a single variable (i.e., degree of disturbance at a site), while all other factors remain unchanged, it should be possible to evaluate the effect of stability without other confounding or undetected influences. Secondly, I wanted to examine whether the simpler communities at the unstable sites had the ability to recover more rapidly from a disturbance, and in turn how that relates to the eigenvalue measurements for each of the sites used in Chapter 9 as a measure of local stability.

MATERIALS AND METHODS

The disturbance field experiment was conducted between 4 February 1989 and 8 April 1989 at Kowai River, Whitewater Stream (both unstable streams), Porter River and Grasmere Stream (both stable streams). No substrate movement (i.e., movement of the fifteen coloured stones) was recorded between these dates and

it appeared to be a very stable period at all four sites (see Chapter 2). Water temperature, depth and current velocity recorded at these four sites during the course of the experiment are given in Table 12.1.

Baskets measuring 30 cm by 15 cm by 10 cm deep, and with 1.25 cm mesh sides were filled with cobbles from the upper bank region of a nearby stream. The cobbles were washed and each basket was filled with five large stones (longest diameter 7-10 cm), and a shovel full of cobbles between 2 and 7 cm diameter. The baskets were buried in the stream beds in a stratified random arrangement (i.e., the three treatments were placed randomly across the stream) with their rims level with the surrounding bed substrata.

A third of the baskets (i.e., 4 per stream) were disturbed each week for nine consecutive weeks (ONE week treatments). This was done by lifting a basket from the substrate (but not out of the stream), shaking it vigorously for 30 seconds, and then replacing it. Another four baskets in each stream were given this treatment every third week for nine weeks (THREE week treatments), and the remaining baskets were left undisturbed (UNDISTURBED treatments). I collected animals dislodged by the shaking procedure on week three of the experiment from half the baskets in each stream (i.e., 4 per stream), by holding a net downstream during the disturbance. Between 62 and 86% of the animals calculated to be in a basket at that time (inferred by interpolating back from the total number of animals collected upon completion of the experiment) were removed during the disturbance.

Table 12.1. Mean current velocity, depth and temperature (with ranges in parentheses) recorded at weekly intervals in Kowai River, Whitewater Stream, Porter River and Grasmere Stream during the disturbance experiment (4 February to 9 April 1989). Current velocity was measured with a Pygmy Gurley current meter 10 cm above the stream bed.

Site	Temperature °C	Depth cm	Current velocity cm s^{-1}
UNSTABLE SITES			
Kowai River	11.4	24	65
	(10-19)	(21-30)	(33-108)
Whitewater Stream	13.7	16	46
	(8-20)	(9-22)	(24-73)
STABLE SITES			
Porter River	9.2	19	65
	(8-11)	(16-24)	(50-88)
Grasmere Stream	13.1	16	80
	(10-19)	(6-24)	(52-97)

At the end of the nine week period, all baskets were lifted into a net (mesh size = 250 μm) held immediately downstream and returned to the laboratory. I also collected four benthic samples from each stream at the same time to act as "controls". This was achieved by placing a 30 cm by 15 cm quadrat (the same area as the baskets) randomly on the stream bed, disturbing the substrate to a depth of 10 cm and collecting the dislodged animals in a net (250 μm mesh) held downstream. All samples were preserved in 10% formalin. One stone from each of the baskets and four from the surrounding substratum were also removed for measurement of periphyton biomass (as described in Chapter 3).

In the laboratory, the cobbles were washed and removed from the remainder of each sample. Organic material including invertebrates in samples from Kowai River and Whitewater Stream were then separated by floatation in a saturated solution of $CaCl_2$, and the remaining fine inorganic sediment was searched for cased caddisflies and molluscs. Floatation was not used for the samples from the other two streams which lacked large amounts of fine inorganic sediment. Animals were removed from samples as in Chapter 4 and identified to the lowest possible level. For Kowai River and Porter River samples counts of animals that passed through 500 μm sieve and were present in densities greater than 200 were obtained by subsampling with a bipartite subsampler. Only animals that were retained by a 500 μm mesh sieve were considered in samples from Whitewater Stream and Grasmere Stream. Differences in the relative abundances of taxa between the > 500 μm and < 500 μm fractions of the Porter River sample were small and as comparisons in this study were either of relative abundances or between treatments within each stream, increasing the size limit of animals sorted at Whitewater Stream and Grasmere Stream was reasoned to have no effect on the analysis or interpretation of results.

Sediments removed from the baskets were separated with sieves into seven size categories based on Cummins (1962). These were: cobbles (> 10 mm and < 20 mm), very very coarse sand (> 2 mm and < 10 mm), very coarse sand (> 1 mm and < 2 mm), coarse sand (> 500 μm and < 1 mm), medium sand (> 250 μm and < 500 μm), fine sand (> 125 μm and < 250 μm) and very fine sand (> 20 μm and < 125 μm). Sediments were dried to a constant weight at 66°C, and ashed at 550°C for 6 hours, the difference in weight before and after ashing gave a measure of the organic content of the sediment fraction.

ANALYSIS

Effects of Disturbance on Community Structure

Treatment effects were examined with the analysis of variance procedures of SAS

(1985). Total numbers of invertebrates, periphyton biomass and Berger-Parker dominance index values were log (x+1) transformed prior to analysis to eliminate any variance heterogeneity. Overall community structure was examined with the detrended correspondence analysis (DECORANA) procedure of the PC-ORD multivariate statistical package (McCune, 1987). Data were log (x+1) transformed prior to analysis. The SAS (1985) stepwise regression procedure was used to examine the relationship between DECORANA axes and variables associated with the treatment effects.

Community Recovery

Colonisation models were fitted to the data using the nonlinear least squares procedure of the SOLO statistical package (Hintz, 1988); significance of fit was tested as outlined by Bates & Watts (1988).

Simulation of random colonisation and disturbance of each of the baskets was performed using a Turbo BASIC program which I wrote (Appendix II). One hundred trials were run for each site.

RESULTS

Effects of Disturbance on Community Structure

Periphyton (i.e., pigment concentration) biomass recorded on stones in the treatment baskets and on the stream bed are plotted in Fig. 12.1. A steady decrease in periphyton biomass was found as disturbance frequency increased. Treatment responses were significantly different ($F = 10.16$, $df = 3,52$, $P < 0.05$), with both stable and unstable sites showing similar patterns ($F = 0.91$, $df = 3,52$, $P > 0.05$).

Stream bed "control" samples contained substantially fewer invertebrates than any of the treatment baskets (approximately half the number that were in the ONE week baskets). In retrospect, this is probably not surprising, as the quadrat samples were collected in a manner very similar to a disturbance and I now know this does not remove all the animals from the substrate. "Controls" are consequently not considered further.

Total numbers of invertebrates and taxa collected in treatment baskets are plotted in Figures 12.2 and 12.3, respectively. Both the number of individuals and the number of taxa increased as disturbance frequency decreased. The number of individuals collected in the baskets was significantly different between the treatments ($F = 22.61$, $df = 2,39$, $P < 0.05$), with a significant difference between the

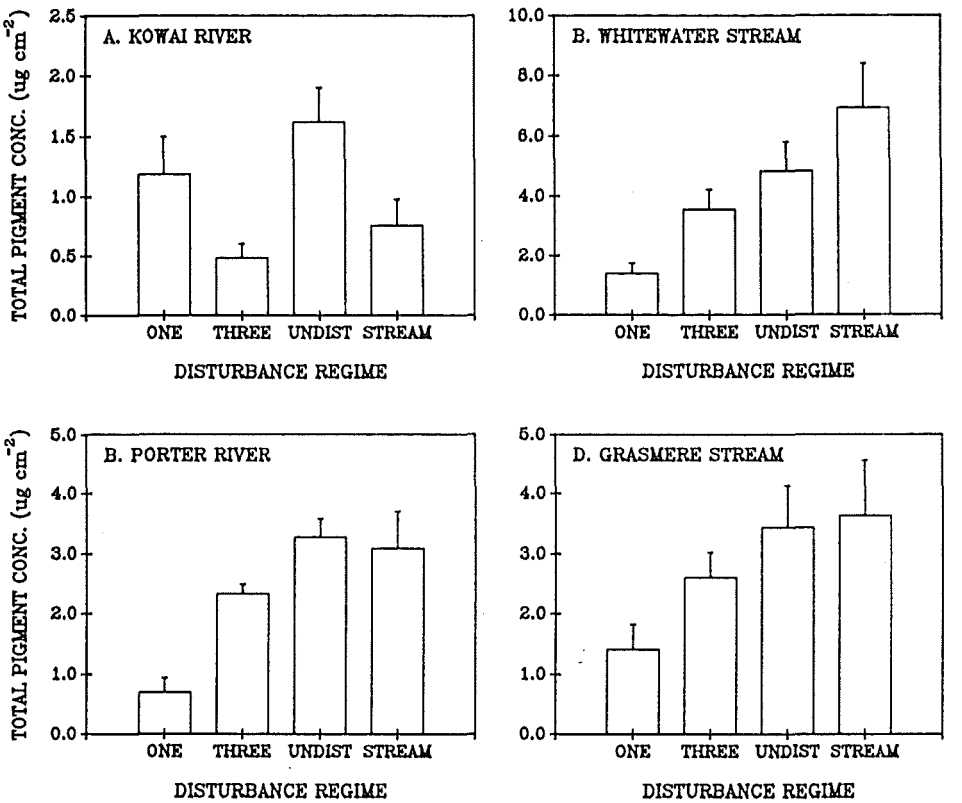


Figure 12.1. Mean concentration of total pigment (chlorophyll *a* and phaeopigment) (± 1 SE) on stones in baskets disturbed every week (ONE), every three weeks (THREE), left undisturbed (UNDIST.) and on the unenclosed stream bed.

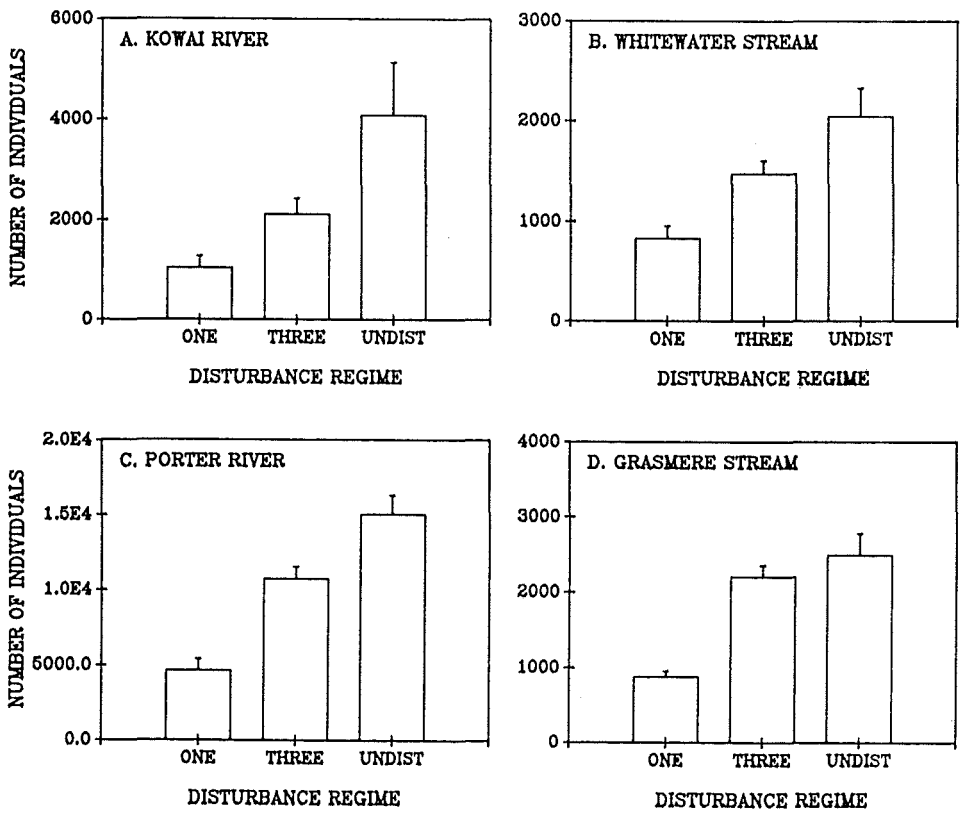


Figure 12.2. Mean number of individuals (± 1 SE) collected in baskets disturbed every week (ONE), every three weeks (THREE) and left undisturbed (UNDIST.).

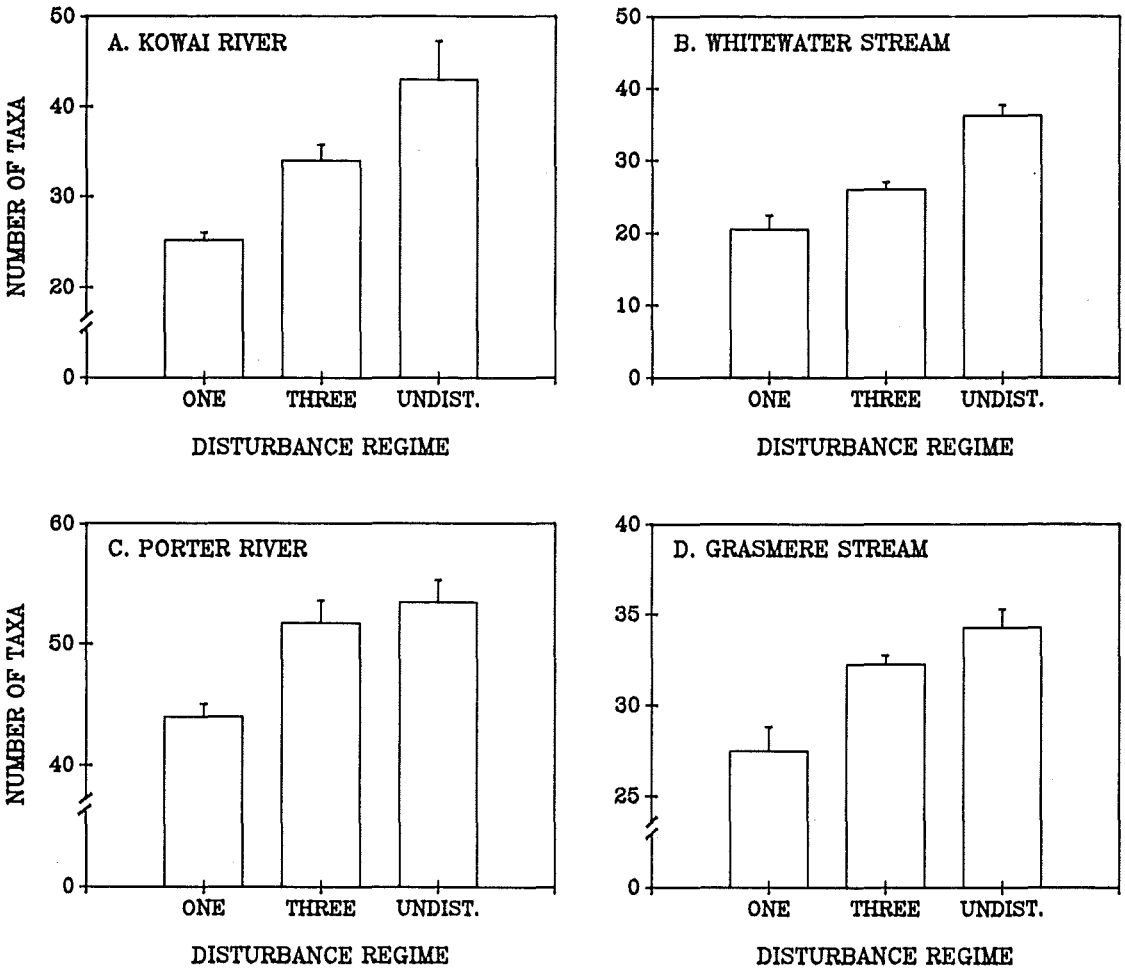


Figure 12.3. Mean number of taxa (± 1 SE) collected in baskets disturbed every week (ONE), every three weeks (THREE) and left undisturbed (UNDIST.).

ONE week disturbance treatments and the other two treatments, which did not differ from each other. A similar pattern was observed at both stable and unstable sites ($F = 0.25, df = 2,39, P > 0.05$). The number of taxa recorded was also significantly different between treatments ($F = 26.47, df = 2,39, P < 0.05$), however, the effect of each treatment on the number of taxa differed between stable and unstable sites ($F = 3.85, df = 1,39, P < 0.05$). The unstable sites exhibited a steady increase in species number across all three treatments, whereas a large increase was found at the stable sites between the ONE and THREE week disturbance regimes, and a very small difference between the THREE week and no disturbance treatments.

I also examined patterns in the two components of diversity with Margalef's index (species richness) and the Berger-Parker dominance index (species evenness). Results are plotted in Fig. 12.4 (Margalef's index) and Fig. 12.5 (Berger-Parker dominance index). Margalef's index increased significantly as disturbance frequency decreased ($F = 23.14, df = 2,39, P < 0.05$), although the pattern differed in stable and unstable streams ($F = 10.30, df = 2,39, P < 0.05$). The un-

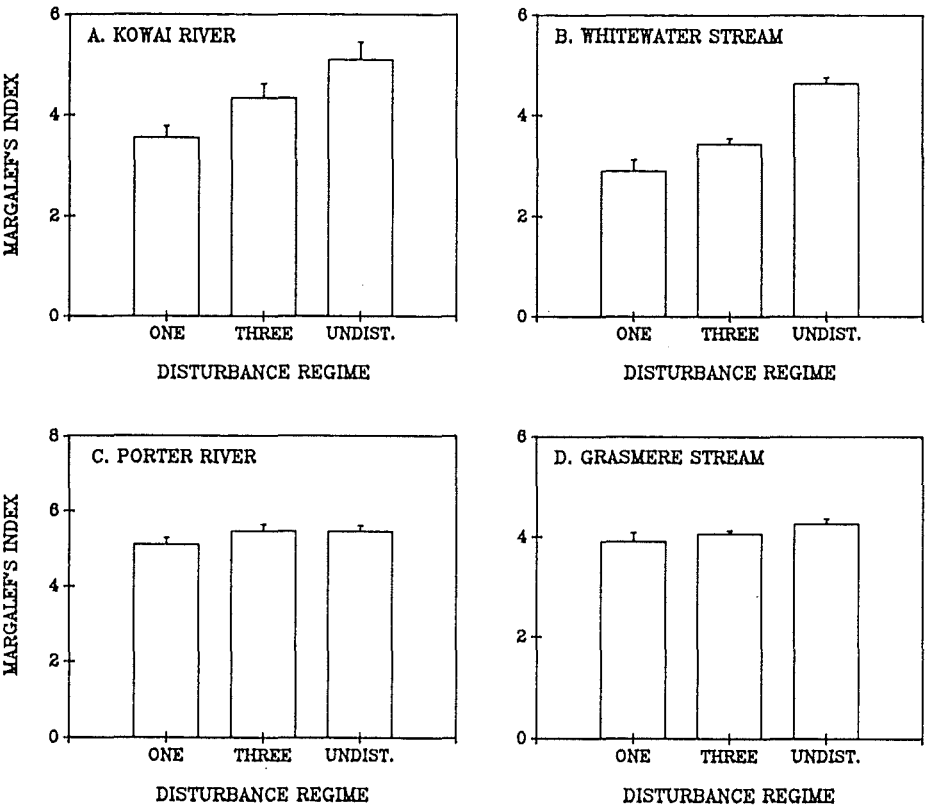


Figure 12.4. Mean values of Margalef's Index (± 1 SE) for the fauna collected in baskets disturbed every week (ONE), every three weeks (THREE) and left undisturbed (UNDIST.).

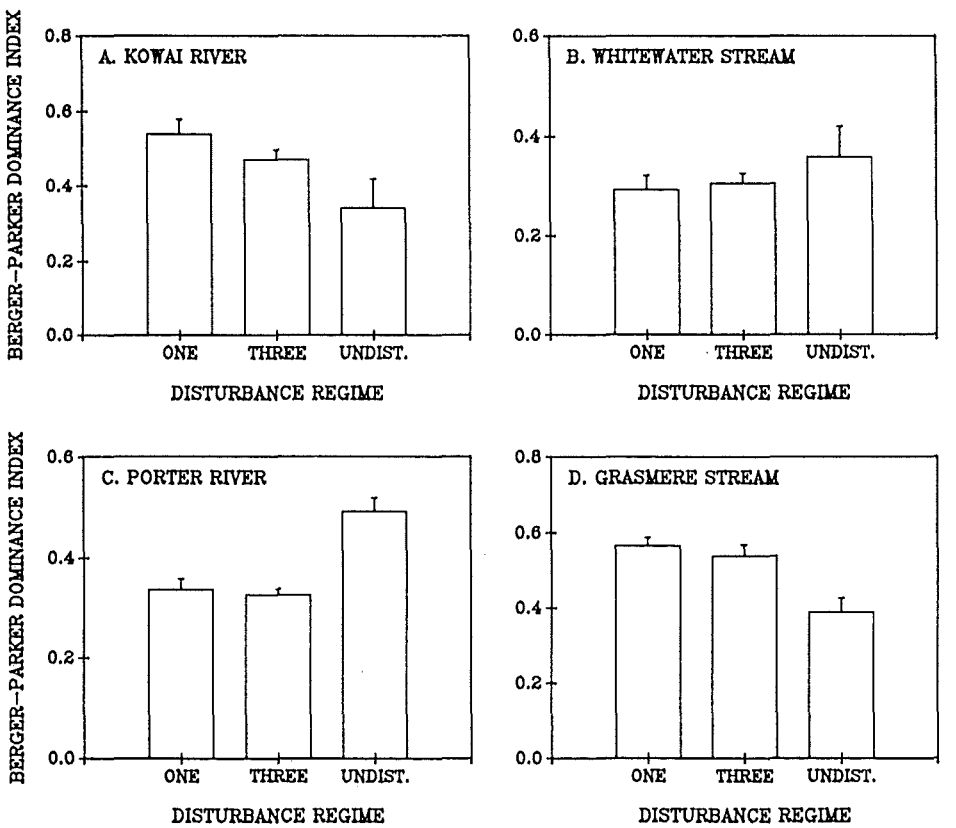


Figure 12.5. Mean values of the Berger-Parker Dominance Index (± 1 SE) for the fauna collected in baskets disturbed every week (ONE), every three weeks (THREE) and left undisturbed (UNDIST.).

stable sites showed a marked increase in species richness across the treatments, but at the stable sites increases were very small. The Berger-Parker dominance index did not change significantly across disturbance treatments (F = 0.31, df = 2,39, P > 0.05). Dominance declined at Kowai River and Grasmere Stream as disturbance frequency decreased, but it increased at Whitewater Stream and Porter River.

Relative abundances of the five most abundant taxa in each of the disturbance treatments are plotted in Fig. 12.6. No marked changes were seen at the unstable

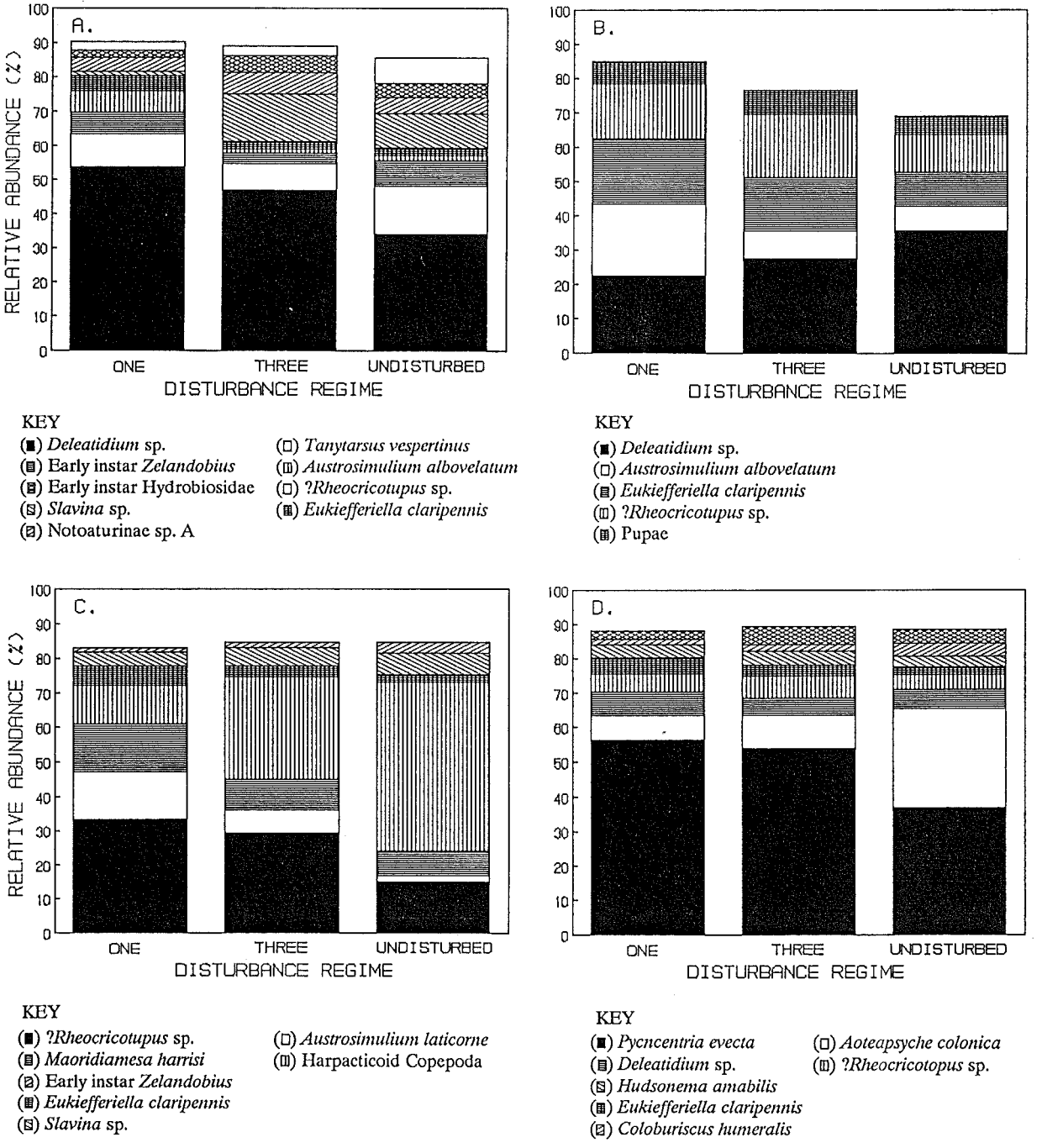


Figure 12.6. Relative abundance of the top five taxa collected in baskets disturbed every week (ONE), every three weeks (THREE) and left undisturbed (UNDIST.), at Kowai River (A), Whitewater Stream (B), Porter River (C) and Grasmere Stream (D).

sites, except for an increase in the relative abundance of *Slavina* sp. in the less disturbed baskets at Kowai River. Both stable sites, however, show a marked increase in the dominance of two taxa (harpactacoid Copepoda at Porter River and *Aoteapsyche colonica* at Grasmere Stream) as time since the last disturbance increased, and a concomitant decrease in the relative abundance of other species.

Overall community structure was examined with DECORANA and a plot of axis one against axis two is given in Fig. 12.7. In general, the baskets representing each treatment in a particular stream occur closest to each other. The ONE week disturbance treatments are grouped together at the far right or left of axis one, the THREE week treatments occur in the centre and the UNDISTURBED treatments are grouped at the opposite end of this axis to the ONE week treatments.

It should be noted that several factors in addition to disturbance effects *per se*, also changed with the treatments and it may be that these led to some of the differences in community structure observed between disturbance treatments. Thus, periphyton biomass increased and the amount of organic and inorganic particulate matter associated with the substrates in each basket also increased

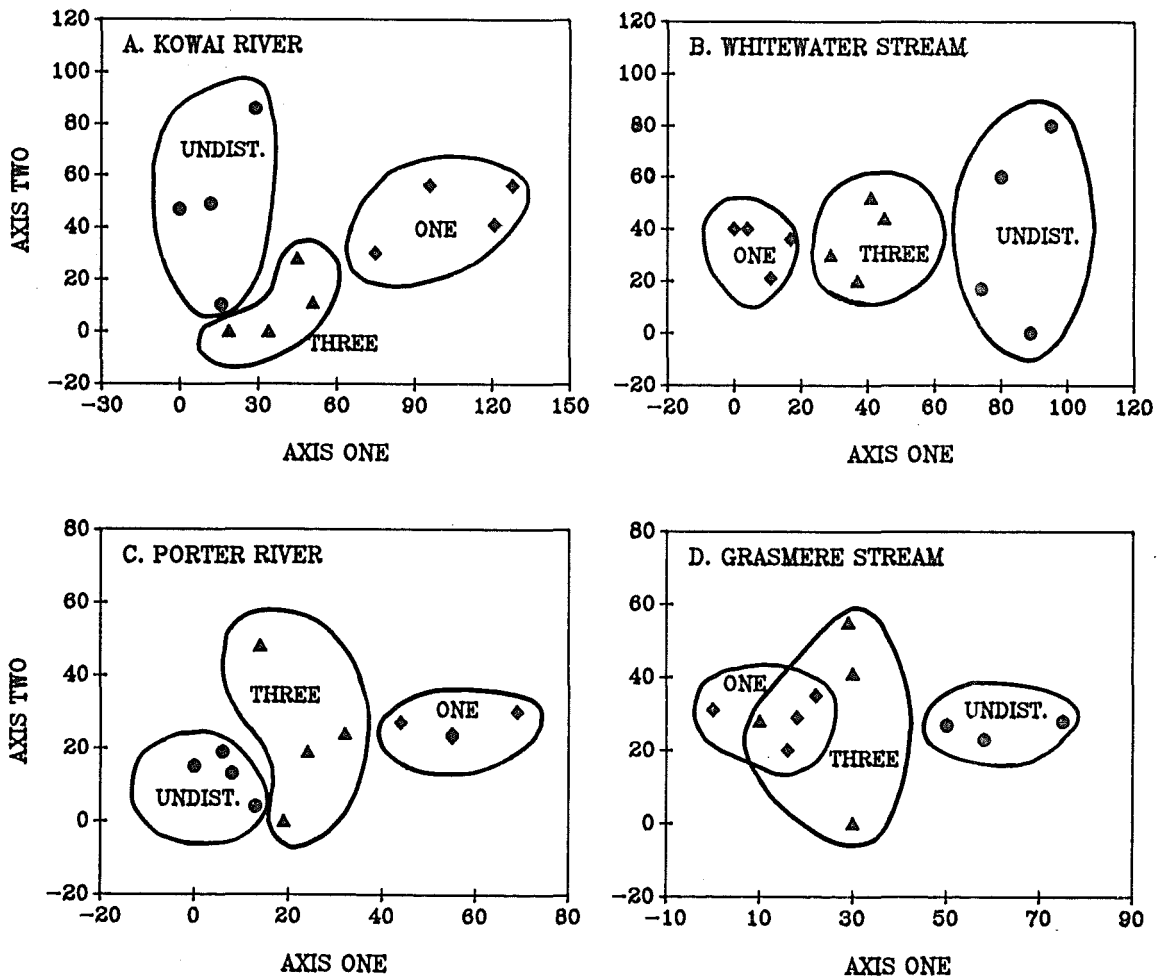


Figure 12.7. Plot of DECORANA axis one against axis two for baskets disturbed every week (♦), every three weeks (▲) and left undisturbed (●).

with decreasing disturbance frequency (Fig. 12.8). I therefore carried out a stepwise regression analysis of axis one, two and three against disturbance frequency, basket position, periphyton biomass, each size component of the organic and inorganic particulates, and the combined size fractions of both the organic and inorganic particulates, to evaluate whether disturbance *per se* was affecting community structure or whether the effect was mediated through secondary factors. Each site had different variables associated with each of its DECORANA axes (Table 12.2), however, disturbance frequency and quantity of organic particulates (particularly fine material) were both commonly associated with community structure.

Community Recovery

As mentioned in Chapter 8, there are two ways in which a community can "survive" a disturbance; it can either resist the disturbance or recover from its effect. Most available evidence suggests that stream invertebrate communities recover from, rather than resist disturbances (see references Chapter 9). However, this

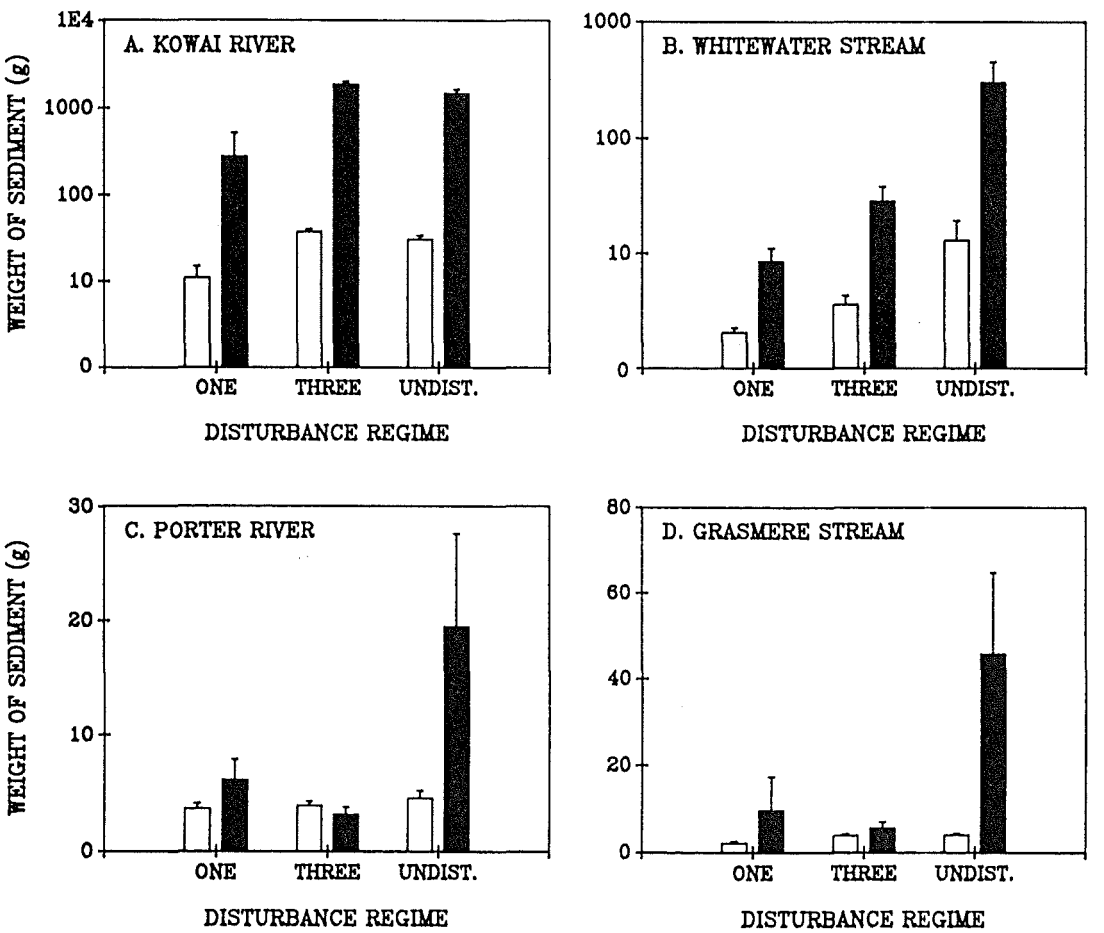


Figure 12.8. Mean weight of organic (open bars) and inorganic (filled bars) sediments (± 1 SE) present in baskets disturbed every week (ONE), every three weeks (THREE) and left undisturbed (UNDIST.).

Table 12.2. Stepwise regression results for DECORANA axes one, two and three against a variety of measurements associated with the disturbance treatments (see main text). Variables were added and removed from the model at a probability level of 0.05. Axes not listed had no significantly correlated variables.

	Variable entered	Parameter estimate	Partial r^2	Model r^2
KOWAI RIVER				
AXIS ONE				
Intercept		99.73		
	Very fine organics	-191.40	0.72	0.72
AXIS TWO				
Intercept		2.38		
	Periphyton biomass	29.27	0.56	0.56
WHITEWATER STREAM				
AXIS ONE				
Intercept		3.88		
	Disturbance treatment	7.56	0.93	0.93
	Periphyton biomass	4.17	0.03	0.96
AXIS TWO				
Intercept		5.31		
	Cobble organics	17.13	0.47	0.47
PORTER RIVER				
AXIS ONE				
Intercept		78.19		
	Fine organics	-114.58	0.74	0.74
	Disturbance treatment	-3.07	0.14	0.88
AXIS THREE				
Intercept		5.31		
	Coarse organics	-52.28	0.72	0.72
GRASMERE STREAM				
AXIS ONE				
Intercept		2.46		
	Coarse organics	240.07	0.69	0.69

does not mean that some invertebrate species are unable to resist some disturbances; in fact it seems likely that some are well adapted for doing so. This contention is supported by my findings that not all animals were removed from baskets by my "relatively severe" disturbances.

The accrual of animals into the baskets can therefore be seen as a combination of recolonisation since the last disturbance and the accumulation of some

species that were able to survive at least some of the disturbances. If the densities of individuals and taxa are plotted against the time available for recolonisation since the last disturbance (i.e., one, three and nine weeks) (Fig. 12.9 and Fig. 12.10, respectively) it is apparent that recolonisation was the major component of

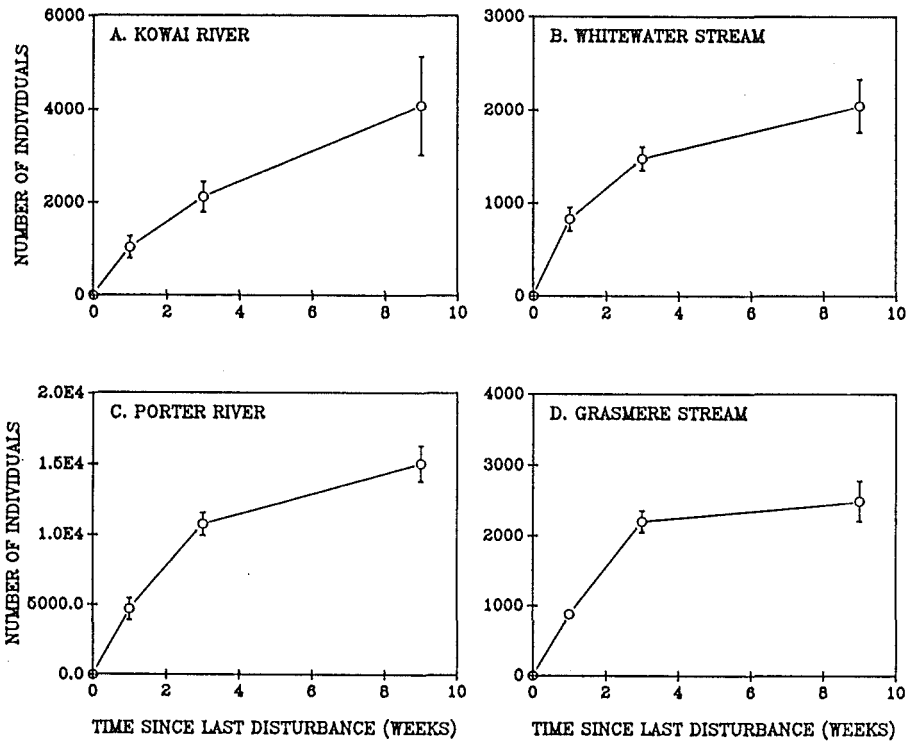


Figure 12.9. Mean number of individuals (± 1 SE) present in each of the treatment baskets as a function of time since the last disturbance.

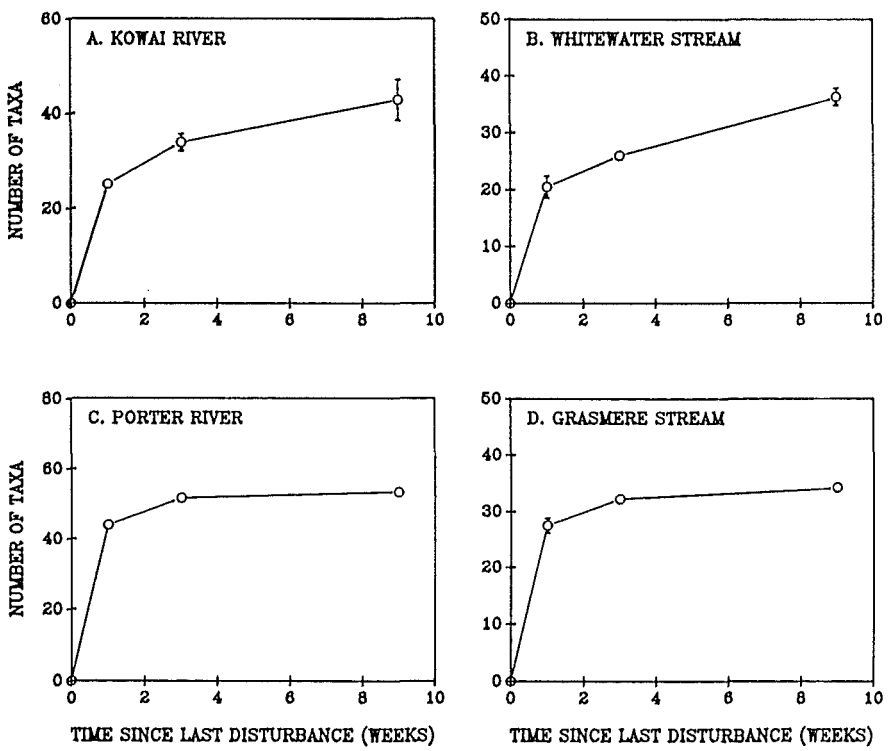


Figure 12.10. Mean number of taxa (± 1 SE) present in each of the treatment baskets as a function of time since the last disturbance.

community (re-) construction. Accumulation of individuals capable of surviving disturbances should have been approximately constant in all three treatments, and no increases or very small increases in densities across treatments would have been observed if it were of primary importance. Although, trade-offs between an ability to survive disturbances and competitive ability may have had some bearing on the outcome.

It is possible to fit models to these curves (Sheldon, 1977, 1984) (they are often termed colonisation curves, although in this case they are strictly speaking not purely colonisation curves as they also include accrual of animals that survive disturbances). The two principal models often fitted to such data are a power function of the form:

$$N_t = at^b$$

where N_t is the population at time t,
and a and b are constants;
and a negative exponential function of the form:

$$N_t = k/m \,.\, (1\text{-}e^{-mt})$$

where N_t is as above
and k and m are constants.

F values denoting the significance of fit of these models to the "colonisation" curves are given in Table 12.3. The "colonisation" curve for the total number of individuals was modelled by both equations at all the sites except Grasmere Stream, where the power function did not fit. However, the negative exponential function was a better fit (i.e., the F value was smaller) for both the stable sites and Whitewater Stream (although in the latter the difference was small). In contrast, Kowai River was modelled better by the power function. "Colonisation" curves for numbers of taxa were only modelled satisfactorily by the power function at the

Table 12.3. F values testing whether the difference in "colonisation" curves for Kowai River, Whitewater Stream, Porter River and Grasmere Stream, and two proposed models ($N_t = at^b$ and $N_t = k/m \,.\, (1\text{-}e^{-mt})$) were significant. Significant differences ($P < 0.05$, $df = 2,12$) are marked with an *.

	Totals		Taxa	
	$N_t = at^b$	$N_t = k/m.(1\text{-}e^{-mt})$	$N_t = at^b$	$N_t = k/m.(1\text{-}e^{-mt})$
UNSTABLE SITES				
Kowai River	0.003	0.046	0.170	3.186*
Whitewater Stream	0.305	0.166	0.104	8.771*
STABLE SITES				
Porter River	2.218	0.067	1.799	0.353
Grasmere Stream	5.471*	1.065	1.062	0.972

two unstable sites, and although both models fitted data for the stable sites they were modelled better by the negative exponential function.

It is apparent from these curves that as time available for recolonisation increases (i.e., time since the last disturbance) the number of taxa and individuals increases. However, the rate of increase slows with time and densities could be expected to eventually reach a plateau, presumably at predisturbance (or "equilibrium") levels. It is not possible to express overall community structure as a single number, however, if community structure was also returning to predisturbance conditions one would expect to find a greater difference between communities (which can be measured) in the ONE week and THREE week treatments than that between the THREE week and UNDISTURBED treatments.

Relative Euclidean distances between communities that developed under the different disturbance regimes did not appear to support this hypothesis, and only Whitewater Stream exhibited a consistent decline in relative Euclidean distance between the communities in the different treatments (Fig. 12.11). However, it

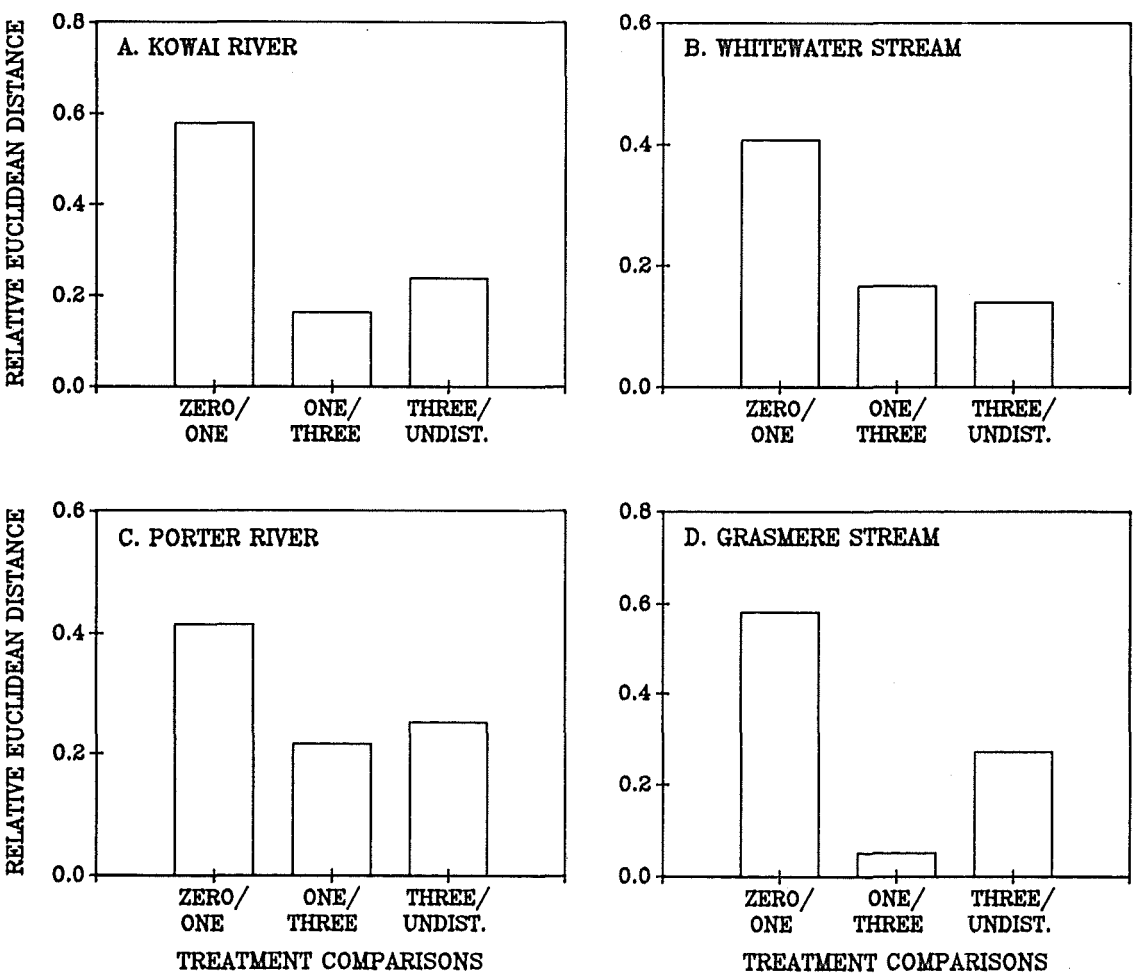


Figure 12.11. Relative Euclidean distance between communities for each of the experimental treatments.

must be remembered that the differences have had varying lengths of time to develop, with one, three and nine weeks for recolonisation in each of the ONE, THREE and UNDISTURBED treatments, respectively. Thus, the THREE week treatment had only two weeks longer than the ONE week treatment for recolonisation, whereas the UNDISTURBED treatment had six weeks longer than the THREE week treatment. The mean rate of change over this period of recolonisation is therefore the difference between the communities divided by the time that that difference has had to develop. Rate of community change is plotted against the mid point of the time interval available for recolonisation (the mean rate of change over the time period is the instantaneous rate of change at the mid point of the time period) in Fig. 12.12. A marked decline in the rate of change is apparent as time since the last disturbance increases.

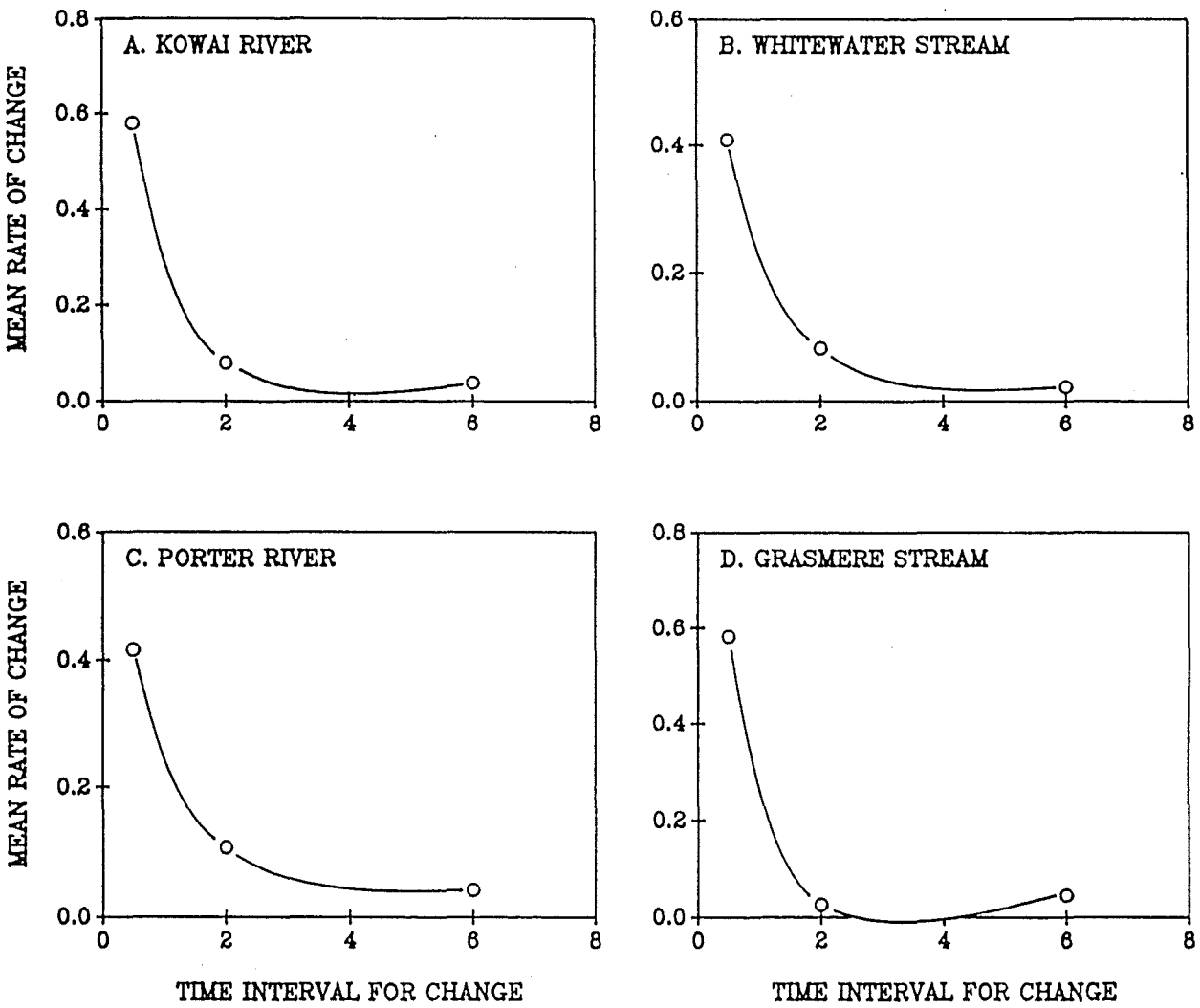


Figure 12.12. Rate of community change as a function of the mid-point of the time available for recolonisation.

The rate of change should approach zero when community structure approaches the conditions found prior to the disturbance. The time taken for this to happen is a measure of the resilience of each of the communities. Analysis of covariance of the curves on a log-log plot reveals that the rate of change decreased with time since the last disturbance ($F = 45.26, df = 1,7, P < 0.05$, $r^2 = 0.87$), but neither the slopes ($F = 0.06, df = 3,4, P > 0.05$) nor the y-intercepts were significantly different between sites ($F = 0.33, df = 3,7, P > 0.05$). That is, all the communities are returning to predisturbance levels at the same rate.

This is quite surprising given that the most stable stream, Porter River, accumulated between four and seven times as many invertebrates as the less stable sites. As the disturbances were conducted in patches of the stream bed, it is likely that the rate of recolonisation was directly proportional to the number of colonists available in the surrounding substrate. Thus, although the more stable sites need to accumulate considerably more invertebrates to return to predisturbance densities, the larger pool of colonists present around the baskets may have facilitated this. To test this hypothesis I modelled the colonisation and disturbance of each basket in an identical fashion to that in the field experiment, but with disturbance and colonisation occurring randomly within the baskets; and compared the results with the outcome of the actual field experiment. Colonists were drawn randomly from a pool of individuals that comprised the maximum density attained by each of the species in any of the baskets (it must be possible for that number of animals to colonise and survive on a basket of this size at some point in time). The percentage of animals removed by the disturbance events was set at 73.93% (the mean of the experimental results).

The mean relative Euclidean distance between randomly constructed communities and differences obtained between communities in the field experiment are plotted in Fig. 12.13. The differences obtained between real communities were 5-65 times higher than those values recorded between randomly constructed communities. Interestingly, values recorded in the experiment at Porter River (the most stable site) were about 50 times greater than those for its randomly constructed communities whereas at the unstable sites differences were much smaller. Thus, although none of these communities could be attributed entirely to chance colonisation the smaller differences between real and random communities at the unstable sites suggests it played a greater role in restructuring communities at these sites than it did at Porter River.

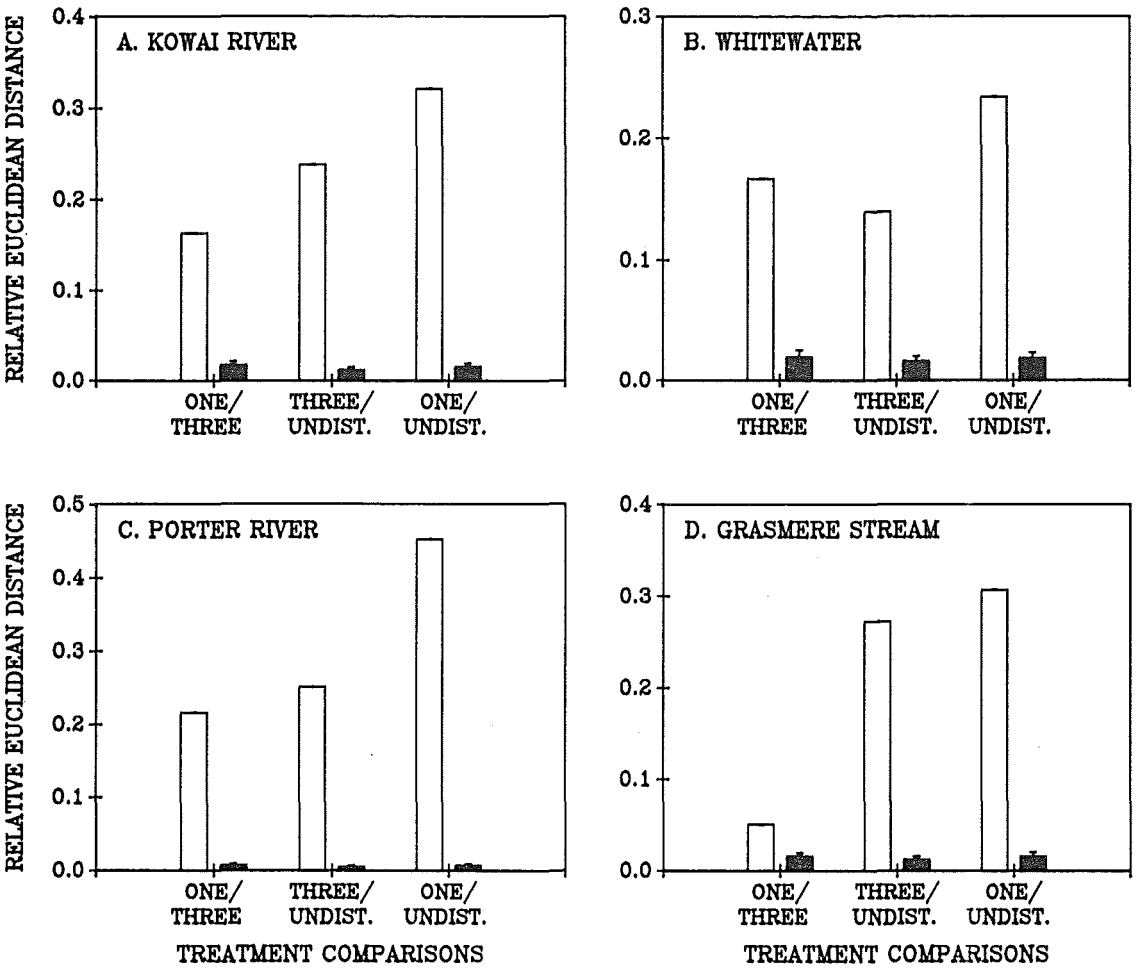


Figure 12.13. Relative Euclidean distance between experimental treatments for real communities (open bars) and randomly constructed communities (filled bars) (± 1 SD).

DISCUSSION

Effects of Disturbance on Community Structure

The finding that both the total number of invertebrates and the number of taxa declined with increasing disturbance frequency supports the conclusions of Chapter 5 that more stable sites have higher numbers of species and invertebrates because they rarely experience major disturbances. However, as in the main study, periphyton biomass was also reduced by increased disturbances and it is therefore unclear whether the lower densities at the unstable sites were primarily the result of disturbance *per se* or whether they were a consequence of disturbances to this food base.

Other experimental studies of disturbances in running waters (e.g., Clifford, 1982; Reice, 1984, 1985; Malmqvist & Otto, 1987; Robinson & Minshall, 1986; Doeg *et al.*, 1989; Lake *et al.*, 1989) have found that disturbances reduce the total

number of invertebrates, although not all showed that the number of taxa were reduced (Reice, 1984, 1985). Experimental studies of the effects of disturbance frequency fall into two categories depending on exactly how the experimenter defines disturbance frequency, or more correctly, how they believe disturbance frequency affects the stream biota. If disturbance frequency is considered to be having an effect because it decreases the time for recolonisation since the last disturbance, then experiments are usually conducted, as in this study, so that different disturbance frequencies are applied to experimental units over a set period of time. This style of experiment has been performed by Robinson & Minshall (1986), who like me found that numbers of invertebrates and taxa declined as disturbance frequency increased. However, when the effect of disturbance frequency *per se* was examined, by Lake *et al.* (1989) (who disturbed patches of stream substrate with different frequencies and then monitored the recolonisation of all the patches for the same length of time), disturbance frequency was found to have no effect on community structure.

My experiment provided no support for the observation (Chapter 6) that the faunas at very stable and unstable sites were dominated numerically by one or two taxa, whereas the faunas at sites of intermediate stability were much more even. Instead, changes in the relative abundances of taxa with respect to disturbance frequency differed between sites regardless of their stability, some (e.g., Porter River) showing increased dominance with decreasing disturbance frequency, while others (e.g., Kowai River) showed the reverse. However, colonisation of experimental patches was not complete at the end of the nine week period so exclusion of any inferior competitors may not have begun to take effect. Similarly, I found no support for the existence of an initially colonising fauna that was eventually replaced by more slowly colonising, but competitively superior species as proposed by the intermediate disturbance hypothesis (Petraitis *et al.*, 1989). No species that colonised the more recently disturbed baskets showed any obvious decline in abundance in the less disturbed baskets, although at Porter River and Grasmere Stream some species (e.g., harpactacoid Copepoda and *Aoteapsyche colonica*) were very slow to colonise, but became increasingly abundant in the undisturbed baskets. Again however, nine weeks may not have been long enough for such changes to occur, or become apparent.

Community Recovery

Although not all animals were removed by my artificial disturbance of the baskets, my results strongly suggest that the principal mechanism enabling the persis-

tence of these communities in the face of small scale physical disturbances is recolonisation, rather than resistance to the disturbance. That different models provided better fits to the "colonisation" curves for the stable and unstable sites, appears to reflect the more rapid accrual of taxa and individuals at the more stable sites, probably because of the larger pool of available colonists in the surrounding substrate. Thus, the negative exponential model, which provided the best fit at the stable sites, approached a plateau (presumably at the carrying capacity of the baskets) more rapidly than the power function, which fitted the data better at the unstable sites. Sheldon (1977) found that both models fitted his data for the colonisation of gravel filled trays in a single stream, while Gore (1979) only fitted the power function, but found that it modelled successfully his data for recolonisation of a reclaimed river channel. However, as I could find no reports of studies that have included comparisons of colonisation curves in streams of differing stability it is difficult to know whether this is a difference peculiar to these streams or whether stream stability does in fact have an effect on recolonisation dynamics.

While the number of taxa and individuals recover more rapidly (or at least build up more rapidly) at the stable sites, the rate of change in overall community structure was very similar in all four streams. This appears to contradict my findings, based on the eigenvalue analysis, reported in Chapter 9 that communities at the more unstable sites should be more resilient. It could be argued that the scale of my experiments may not be appropriate for examining the resilience of these communities. Minshall (1988) claimed that experiments on community recovery in streams should be conducted with whole stream disturbances, however while a flood may disturb an entire stream, most spates appear to disturb the substrate patchily, particularly with respect to substrate size (Doeg *et al.*, 1989 and personal observations). Therefore given the scale at which most spates affect the stream bed, it would seem that substrate patches (as used in this study) are appropriate units for studies of most physical disturbances experienced by these benthic communities. Furthermore, the eigenvalue analysis refers to local stability conditions (i.e., the effect of small disturbances) and although it is difficult to relate mathematical definitions to the real world, my experimental disturbances would certainly appear to be small.

The observation that communities at the unstable sites had eigenvalues indicative of more resilient communities, was made however by ignoring a number of eigenvalues that indicated that the communities were not stable in the first place (i.e., they would never recover fully from a disturbance). This is clearly not the case, the communities in these streams did recover quickly from disturbances,

at least at the scale of this experiment. It seems more likely that the concept of local stability (as assessed with the eigenvalues) is not an appropriate measure of resilience for these communities, either because of their open nature and/or their patchy distribution (see Chapter 9 for a discussion).

Recolonisation of substrate patches following my disturbances could not be explained by simple random accumulation of individuals from the pool of available colonists. Some taxa such as *Deleatidium* and *Austrosimulium* were quick to arrive in recently disturbed patches, whereas others such as harpactacoid Copepoda and *Aoteapsyche colonica* were slower to colonise but gradually became more dominant, although densities of the initial colonists were not reduced as a result. However, exactly what factors may have led to these deviations from simple random accumulation are still unknown.

In summary, the apparently less complex communities that exist at the unstable sites do not have a greater ability to recover from disturbances at the scale of my substrate baskets, than the more complex communities at the stable sites. Rather, all the communities in these streams appeared to have an inherent ability to cope with disturbances of this nature, and it may be that the stream environment in general places constraints on benthic communities, independently of the stability of those streams, which in turn enables the communities to recover rapidly from disturbances of this kind (such as the drift of colonists and/or food resources downstream to disturbed areas). The persistence of the communities in the face of these patch disturbances was dominated by recolonisation, although this was not the result of simple random accumulation of individuals.

CHAPTER 13

FOOD WEB CHARACTERISTICS

"... Food web analyses of lotic communities are clearly daunting in their complexity... "

Power *et al.*, 1988

INTRODUCTION

Since Cohen (1978) re-introduced the concept of food webs into the ecological literature (the ecological significance of food webs was originally introduced in the 1920's by Charles Elton (Elton, 1927)), food web studies have become a small growth industry (Lawton, 1989). The majority of these studies have involved analysis and re-analysis of various sized subsets of 113 webs that have been compiled from a wide range of sources of ecological literature, although more recently there has been a trend towards collecting new data (e.g., Pimm & Kitching, 1987; Warren, 1989; Winemiller, 1990).

The compiled food webs (Briand & Cohen, 1987) comprise a diverse array of taxa, differ markedly in sampling and taxonomic precision, and were recorded over a wide range of temporal and spatial scales (Warren, 1989). However, the underlying structure of these food webs appears to conform to a number of regularities (Cohen, 1978; Pimm, 1982; Lawton & Warren, 1988; Lawton, 1989). These include a lack of loops where species A eats species B eats species C eats species A (Pimm, 1982; Pimm & Lawton, 1983), food chains are typically short (Elton, 1927; Hutchinson, 1959; Pimm & Lawton, 1977; Pimm, 1982), and there is a hyperbolic decrease in connectance (defined as the number of realised links, divided by the number of possible links) as species number increases (Rejmanek & Stary, 1979; Yodzis, 1980; Pimm, 1982; Cohen *et al.*, 1985). Furthermore, the proportion of top, intermediate and basal species present is relatively constant and independent of the total number of species (Briand & Cohen, 1984; Cohen & Briand, 1984), and the ratio of predator species to prey species is roughly constant (Cohen, 1977, 1978; Jeffries & Lawton, 1985). The proportion of links between basal, intermediate and top species is also independent of species number (Cohen & Briand, 1984). Omnivores are relatively rare (Pimm & Lawton, 1978, 1983; Pimm, 1982), although webs of insects and parasitoids often have abundant and complex omnivory (Pimm & Lawton, 1978, 1983; Pimm, 1982). Finally, food webs tend to be "interval" (Cohen, 1977, 1978, 1983) such that overlap in prey use by predators can be expressed in one dimension. A variety of hypotheses have been put forward to explain many of these patterns (for reviews see Pimm, 1982; Lawton, 1989).

The specific nature of the habitat has been shown to influence both overall food web structure (Briand, 1983, 1985) and specific characteristics of the web, for example, food chains appear to be shorter in "two-dimensional" habitats (e.g., grassland) than in "three-dimensional" ones (e.g., lakes) (Briand & Cohen, 1987).

Environmental variability has also been shown to affect food web structure;

food webs from "constant" environments have proportionally more links between basal and top species than webs from "fluctuating" environments, and show greater variance in many of the web components (e.g., proportion of top, intermediate and basal species) (Briand & Cohen, 1984; Cohen & Briand, 1984). Connectance also appears to be lower in "fluctuating" environments (Briand, 1983; Cohen *et al.*, 1985) where food chains are typically shorter (Briand & Cohen, 1987). However, these generalizations have been derived from food webs taken from a wide range of habitats, and are therefore confounded by both the influence of habitat structure and the subjective assessment of environmental variability (based on the impressions of the original authors who drew up the webs) (Lawton, 1989). When Briand & Cohen (1987) factored out the influence of habitat structure they found "constant" environments did not support markedly longer food chains, although sample sizes were so small when this was done that no firm conclusions could be drawn.

In this chapter, I examine the characteristics of the food webs collected at each of my study sites on five separate occasions. It was therefore possible to examine changes in web characteristics along a continuum of decreasing environmental stability while removing the confounding influence of habitat differences encountered in the studies of Briand (1983, 1985) and Briand & Cohen (1987).

While food web studies and food web theory may have developed into a "growth industry", stream ecologists have generally avoided this theoretically orientated approach to studies of trophic organisation (but see Hildrew *et al.*, 1985), in favour of examining functional feeding group organisation. Initially proposed by Cummins (1973) this approach has been bolstered by the river continuum concept (Vannote *et al.*, 1980) and the controversy surrounding its general applicability (Winterbourn *et al.*, 1981; Townsend & Hildrew, 1984; Lake *et al.*, 1985). Thus a number of authors have examined spatial and temporal patterns in the functional feeding group organisation of stream invertebrate communities (e.g., Hawkins & Sedell, 1981; Dudgeon, 1984; Marchant *et al.*, 1985; Bunn, 1986). I have therefore also examined functional feeding group organisation of the invertebrate communities present at each of my sites and related it to differences in the environmental stability of those sites.

MATERIALS AND METHODS

Compilation of Food Webs

The samples of invertebrates collected at each site on five separate sampling occasions (see Chapter 4) formed the basis of the food webs. Taxa were not

lumped into trophic species, but considered at the same taxonomic level considered in the rest of the study. If invertebrates were represented by only one individual in these collections they were removed from the web construction. This was done to maintain consistency with the analysis in Chapter 9, and because such rare species are unlikely to have a significant impact on food web structure.

The presence of vertebrate predators in the webs was assessed by electrofishing each of the study sites in October 1990, and by the chance collection of fish whenever the opportunity arose on other sampling occasions. The fish collected by electrofishing and other methods during the course of the study are listed in Table 13.1. Fish were assumed to be present throughout the course of the study (i.e., if they were collected at a site they occurred in the webs at that site on all five sampling occasions).

Feeding links were assessed by a variety of methods including examination of the available literature, personal observations and gut analysis. Links were not included unless there was strong evidence to suggest they exist. However, if a link was recorded it was assumed to exist whenever those two species occurred together. Thus the webs could be considered maximally connected, although only trophic links were included (competitive links are considered in Chapter 9).

The guts of most of the fish collected (i.e., all those big enough) were examined (Appendix IV). Eight publications that reported on the diets of the fish species collected, and 23 publications that reported on the diets of the invertebrates collected were also considered. The majority of these studies were conducted in the general geographical area of my study and several were conducted at or near my actual study sites. Many were conducted over several seasons and reported little or no seasonal change in diet of the species considered. They suggest that seasonal changes in dietary links of many animals are unlikely to occur unless food items are not present at a particular site in particular seasons. Web

Table 13.1. Fish collected by electrofishing at all study sites in October 1990, and incidentally (in parentheses) during the course of the study.

	UNSTABLE SITES					STABLE SITES					
ISH	Kowai River	Whitewater Stream	Dry Stream	Craigieburn Cutting Stream	Bruce Stream	Porter River	Slip Spring	Cora Lynn Stream	Middle Bush Stream	Grasmere Stream	Lake Grasmere
nguilla dieffenbachi	-	-	-	-	-	-	-	-	-	9 (5)	- (1)
'alaxias brevipinnis	2 (1)	-	-	-	-	1	-	1 (1)	-	1	-
'alaxias vulgaris	1 (2)	3 (1)	- (2)	-	1	-	-	14	-	-	-
'alaxias paucispondylus	-	-	- (1)	-	6	7	-	-	-	-	-
'obiomorphus breviceps	-	2	-	-	-	-	-	-	-	-	17 (4)
ılmo trutta	-	-	-	-	-	1 (4)	12	-	-	1	2
ncorhynchus mykiss	-	2	-	-	-	1	-	-	-	-	-
OTAL	3 (6)	7 (8)	-(3)	-	7	10 (14)	12	15 (16)	-	11 (16)	19 (24)

construction from a seasonal perspective, but based on pooled dietary information thus seems to be a reasonable procedure.

The guts of all taxa collected at Kowai River (number of taxa (S) = 28), Porter River (S = 49), Whitewater Stream (S = 37) and Grasmere Stream (S = 44) in the October 1987 sample were examined. Any other taxa for which there were insufficient records of gut contents in the literature, and for which there were more than a few individuals were also examined. The guts of ten individuals of each taxon (or all individuals if fewer than ten were collected) were teased out, dispersed for 45-60 seconds in an ultrasonic cleaner and filtered on to a 0.45 μm Millipore filter. Filters were mounted on slides with lactophenol-PVA stained with Lignin Pink and allowed to clear for a minimum of seven days at 37°C. The slides were then examined under 450x magnification with a phase contrast microscope, and food items present anywhere on the filter surface were recorded. Individuals representing different size groups of common taxa were considered separately.

The results of my gut analyses were consistent with records of gut contents for these taxa in the literature. Not unexpectedly, there were differences in the relative abundance of many food categories between sites and between size groups for many taxa, however, the presence or absence of food categories did not appear to differ between sites or between most size groups (where applicable). Site and size group differences, at least in the presence of dietary links (the strength of these links is probably a different story), therefore appear to be minimal and are probably largely a consequence of certain food items being present or absent at a particular site. Web construction from a spatial perspective (i.e., site differences) based on the pooled dietary information therefore also appears to be a realistic procedure.

Other sources of dietary information included personal observations of M.J. Winterbourn, my own observations in the field, some laboratory trials and a preliminary serelogical investigation of the diet of *Neppia montana* (unpublished data). Despite all these sources, seven taxa remain for which there is little or no New Zealand information. These are Staphylinidae, Ceratopogonidae, *Nothodixa* sp., Stratiomyidae, *Limnophora* sp., Thaumaleidae and Psychodidae. They were assigned diets based on information in Merritt & Cummins (1984) and/or references therein.

All possible food chains present at a site were constructed using a Turbo BASIC program which I wrote and the food web characteristics recorded from these.

Definitions

Species and linkage definitions follow those of Pimm (1982), Cohen & Briand (1984) and Briand & Cohen (1984); that is, top species are those that feed on others but are not fed upon, intermediate species are fed on and feed upon others, and basal species are those that are fed upon but do not feed on others. An "omnivore" is defined as a species that feeds on more than one level in the food chain (Pimm, 1982). As predator-prey ratios have been calculated in two distinct ways by other workers, both techniques were used. Cohen's (Cohen, 1977, 1978) ratio defines "predators" as species that consume others, thus animals that feed upon others and are themselves fed upon are counted twice, once as "predators" and once as "prey". Jeffries & Lawton (1985), in contrast, restricted their ratio to invertebrates, thus "prey" species are detritivores, herbivores and fungivores and "predators" eat "prey". Those animals that were predominantly carnivorous were considered to be "predators".

Functional Feeding Groups

Functional feeding group analysis was conducted using only the invertebrate data (Appendix I). Any species with a density lower then 1 per 0.1 m^2 was excluded from the analysis to maintain consistency with the food web analysis. Functional feeding categories were designated based on modifications made by Cowie (1980) to Cummins (1973) original four categories (i.e., shredders, collector-gatherers, scrapers and predators). Thus seven categories were recognised: collector/ browsers (an amalgamation of Cummins' collector-gatherer and scraper groups), filterers, shredders, predators, piercers (e.g., Nematoda), parasites, and non-feeding organisms (e.g., pupae).

Statistical Analysis

Regression analysis was carried out using the GLM procedure of SAS (1985). Multivariate ordination of food web characteristics (see results) was carried out using the PCord statistical package (McCune, 1987). What environmental, biological or stability characteristics these axes corresponded to was then assessed with the stepwise regression and Pearson product moment correlation procedures of SAS (1985). Stepwise regression was carried out using 26 biological, chemical, physical and stability measurements as listed in Table 13.7. Spot measurements are those made at the time of collection, or in the month prior to the collection of

samples. The critical probability for addition and removal of variables to the model was set at 0.05. The same variables were used in the correlation analysis.

A similar procedure was carried out for the number of species, number of individuals and the relative abundance of each of the six functional feeding group categories, although the latter two were log (x+1) transformed prior to analysis.

RESULTS

Food Web Characteristics

The average, coefficient of variation, and range for the mean, maximum and modal food chain length are listed in Table 13.2. The mean, maximum and modal food chain length are also plotted against overall (multivariate) stability in Fig. 13.1. All three showed a significant decrease with a decrease in stability ($F = 11.76, df = 1,49, P < 0.05, r^2 = 0.33$; $F = 113.41, df = 1,49, P < 0.05$, $r^2 = 0.37$; and $F = 11.79, df = 1,49, P < 0.05, r^2 = 0.30$ for average, maximum and modal chain length, respectively).

The average, coefficient of variation and range of each of the five trophic categories (basal species, herbivores, top species, intermediate species and omnivores) as a fraction of the total species, collected at each of the sites, is recorded in Table 13.3. These are plotted against total species number in Fig. 13.2 and the results of the regression analyses of these are plots listed in Table 13.4. All five showed significant trends. Fraction of basal species and fraction of top species decreased as species number increased, whereas fraction of intermediate species, herbivores and omnivores increased.

The relationship between the fraction of each of these categories and overall (multivariate) stability are plotted in Fig. 13.3 with the results of the regression analyses given in Table 13.4. Again, the basal and intermediate species exhibit the strongest patterns. The fraction of basal species increases as stability decreases and the fraction of intermediate species and herbivores decreases. The fractions of top species and omnivores show no significant trends with stability.

The total number of food web links is plotted against species number in Fig. 13.4. This increased significantly ($F = 179.36, df = 1,53, P < 0.05, r^2 = 0.77$) as species number increased. The ratio of links to species number as a function of overall stability is plotted in Fig. 13.5. This exhibited a significant decrease with a decrease in stability ($F = 18.81, df = 1,49, P < 0.05, r^2 = 0.43$).

The average proportion of each of the component link types (top-basal, top-intermediate, intermediate-intermediate and intermediate-basal) are listed in

Table 13.2. Averages, coefficients of variation and ranges for mean, maximum and modal food chain length, connectance, complexity and the predator-prey ratios of both Cohen and Jeffries & Lawton, for food webs collected at each of my study between October 1987 and October 1988.

Sites	Food chain length					Predator/prey ratio	
	Average	Maximum	Mode	Connectance	Complexity	Cohen's ratio	Jeffries & Lawton's ratio
UNSTABLE SITES							
Kowai River	3.906	5	4	0.275	7.962	0.908	0.249
	8.95	14.14	0	6.75	17.21	8.52	42.22
	(3.47-4.43)	(4-6)	(4-4)	(0.25-0.29)	(6.17-9.31)	(0.80-1.00)	(0.12-0.38)
Whitewater Stream	4.365	6	4.4	0.288	9.023	1.047	0.248
	14.12	20.41	20.33	12.72	24.25	15.34	68.63
	(3.39-4.94)	(4-7)	(3-5)	(0.23-0.34)	(5.29-10.94)	(0.80-1.24)	(0-0.47)
Dry Stream	3.823	4.6	3.8	0.243	8.307	0.993	0.295
	14.53	19.44	11.77	13.88	27.06	12.95	61.55
	(2.85-4.17)	(3-5)	(3-4)	(0.20-0.28)	(4.78-10.21)	(0.77-1.10)	(0-0.43)
Craigieburn Cutting Stream	3.092	4	3.2	0.242	5.604	0.930	0.278
	25.89	35.36	34.23	15.93	44.54	25.52	37.70
	(2.00-3.72)	(2-5)	(2-4)	(0.20-0.30)	(2.25-7.84)	(0.63-1.13)	(0.14-0.36)
Bruce Stream	2.962	3.6	2.8	0.296	4.249	0.815	0.090
	12.33	15.22	15.97	23.52	40.28	18.13	106.55
	(2.36-3.26)	(3-4)	(2-3)	(0.20-0.38)	(2.20-5.71)	(0.67-1.00)	(0-0.22)
STABLE SITES							
Porter River	4.229	5.8	4.2	0.217	12.083	1.135	0.350
	6.82	14.43	10.65	5.28	8.63	6.04	16.12
	(3.89-4.59)	(5-7)	(4-5)	(0.20-0.23)	(10.34-13.13)	(1.03-1.20)	(0.27-0.42)
Slip Spring	3.747	5	3.8	0.202	9.850	1.125	0.428
	2.82	0	11.77	6.11	15.07	4.88	7.68
	(3.58-3.83)	(5-5)	(3-4)	(0.19-0.22)	(7.30-11.04)	(1.03-1.18)	(0.38-0.47)
Cora Lynn Stream	3.812	5.4	3.8	0.186	8.826	1.015	0.214
	19.76	28.09	22.02	6.87	27.63	9.73	50.48
	(3.01-4.70)	(4-7)	(3-5)	(0.17-0.20)	(6.07-11.42)	(0.88-1.12)	(0.11-0.36)
Middle Bush Stream	3.673	5	4	0.172	6.591	1.025	0.209
	2.02	0	0	15.30	7.51	3.16	15.45
	(3.59-3.77)	(5-5)	(4-4)	(0.15-0.22)	(5.90-7.14)	(0.97-1.06)	(0.17-0.25)
Grasmere Stream	4.514	6.4	4.4	0.229	10.669	1.078	0.281
	7.94	8.56	12.45	11.70	15.17	8.45	42.01
	(3.99-4.88)	(6-7)	(4-5)	(0.19-0.26)	(8.56-12.43)	(1.00-1.22)	(0.18-0.46)
Lake Grasmere	5.186	8	5.2	0.225	10.986	1.120	0.300
	5.10	8.84	8.6	5.09	11.37	7.23	29.15
	(4.84-5.57)	(7-9)	(5-6)	(0.21-0.24)	(9.74-12.87)	(1.03-1.21)	(0.20-0.41)

Table 13.5. These are plotted against total number of species in Fig. 13.6, and the results of regression analyses of these plots recorded in Table 13.6. The fraction of top-basal and intermediate-intermediate links were the only two to show significant trends (although top-intermediate and intermediate-basal links also showed significant decreases if one outlier web (Craigieburn winter sample) was removed from the analysis (F = 19.71, df = 1,52, $P < 0.05$, r^2 = 0.27 for both plots). The fraction of top-basal links decreased as species number increased and the fraction of intermediate-intermediate links increased. The fraction of each of the trophic links are plotted against overall stability in Fig. 13.7 and the regression analyses for these plots are recorded in Table 13.6. All showed significant trends, although they were not particularly strong. The fraction of top-basal, top-inter-

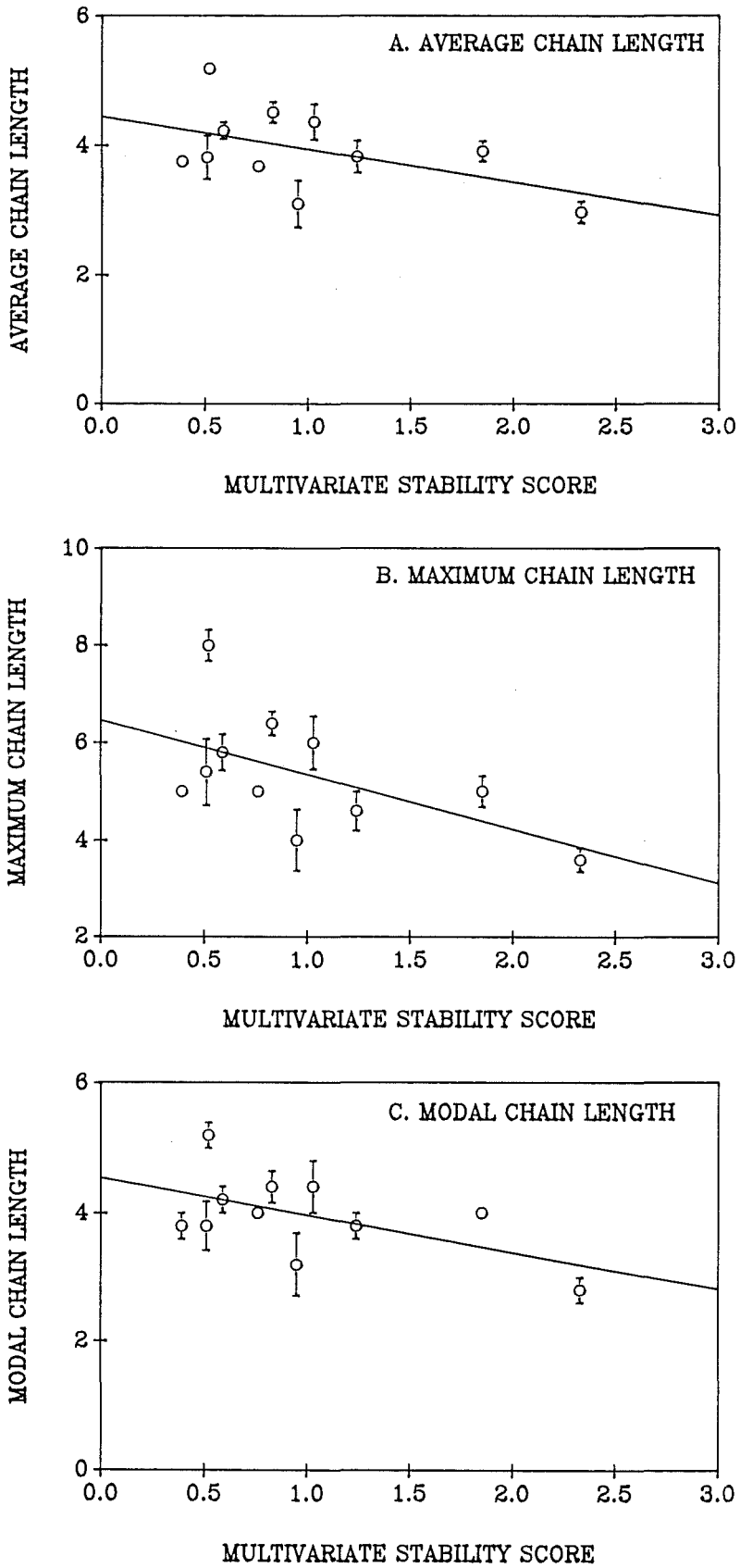


Figure 13.1. Average, maximum and modal food chain length as a function of overall stability (multivariate stability score). Plotted values are averages for the seasonal measures ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the following equations: average chain length = 3.95 - 0.51(stability score), r^2 = 0.33; maximum chain length = 5.57 - 1.12(stability score), r^2 = 0.37 and modal chain length = 4.03 - 0.57(stability score), r^2 = 0.30.

Table 13.3. Mean, coefficient of variation and range for the proportion of each of the five trophic categories collected at my study sites between October 1987 and October 1988.

Sites	Proportion of				
	Basal species	Herbivores	Top species	Intermediate species	Omnivores
UNSTABLE SITES					
Kowai River	0.274	0.527	0.131	0.578	0.199
	15.94	10.50	40.84	12.25	21.07
	(0.22-0.33)	(0.48-0.61)	(0.08-0.21)	(0.50-0.69)	(0.14-0.24)
Whitewater Stream	0.210	0.542	0.156	0.634	0.216
	33.97	6.61	28.09	16.90	19.90
	(0.16-0.33)	(0.50-0.59)	(0.10-0.22)	(0.44-0.70)	(0.17-0.27)
Dry Stream	0.229	0.548	0.142	0.629	0.193
	16.94	11.89	28.37	11.92	35.36
	(0.20-0.29)	(0.48-0.63)	(0.11-0.21)	(0.50-0.68)	(0.08-0.25)
Craigieburn Cutting Stream	0.238	0.594	0.363	0.399	0.116
	60.21	14.87	35.04	66.84	94.06
	(0.13-0.44)	(0.44-0.66)	(0.25-0.56)	(0.00-0.61)	(0.00-0.23)
Bruce Stream	0.350	0.438	0.265	0.386	0.140
	34.05	29.04	45.82	53.85	39.09
	(0.24-0.50)	(0.25-0.55)	(0.14-0.45)	(0.09-0.57)	(0.09-0.21)
STABLE SITES					
Porter River	0.170	0.559	0.197	0.633	0.221
	13.51	2.59	10.27	4.83	17.43
	(0.15-0.21)	(0.54-0.57)	(0.17-0.22)	(0.58-0.66)	(0.19-0.27)
Slip Spring	0.171	0.563	0.222	0.607	0.149
	13.55	2.39	6.72	3.37	13.79
	(0.15-0.21)	(0.55-0.58)	(0.21-0.24)	(0.58-0.62)	(0.11-0.16)
Cora Lynn Stream	0.172	0.644	0.234	0.594	0.169
	21.00	6.60	20.43	14.16	38.30
	(0.13-0.23)	(0.58-0.69)	(0.18-0.30)	(0.47-0.68)	(0.10-0.25)
Middle Bush Stream	0.129	0.721	0.301	0.570	0.150
	11.17	2.85	13.25	7.09	13.04
	(0.12-0.15)	(0.69-0.74)	(0.26-0.37)	(0.51-0.62)	(0.13-0.17)
Grasmere Stream	0.172	0.598	0.128	0.699	0.208
	7.27	7.11	14.28	2.20	23.25
	(0.15-0.19)	(0.54-0.64)	(0.11-0.15)	(0.68-0.72)	(0.14-0.26)
Lake Grasmere	0.152	0.603	0.197	0.651	0.208
	10.11	4.76	5.69	1.81	21.92
	(0.13-0.17)	(0.56-0.64)	(0.18-0.21)	(0.64-0.67)	(0.13-0.24)

mediate and intermediate-basal all increased with a decrease in stability, whereas the fraction of intermediate-intermediate decreased.

Connectance is plotted against total number of species in Fig. 13.8. It showed a significant decrease as the number of species increased ($F = 25.23$, $df = 1,53$, $P < 0.05$, $r^2 = 0.32$), and a significant increase (Fig. 13.9) as overall stability decreased ($F = 33.98$, $df = 1,49$, $P < 0.05$, $r^2 = 0.42$). However, complexity (measured as connectance x total number of species) showed a significant decrease

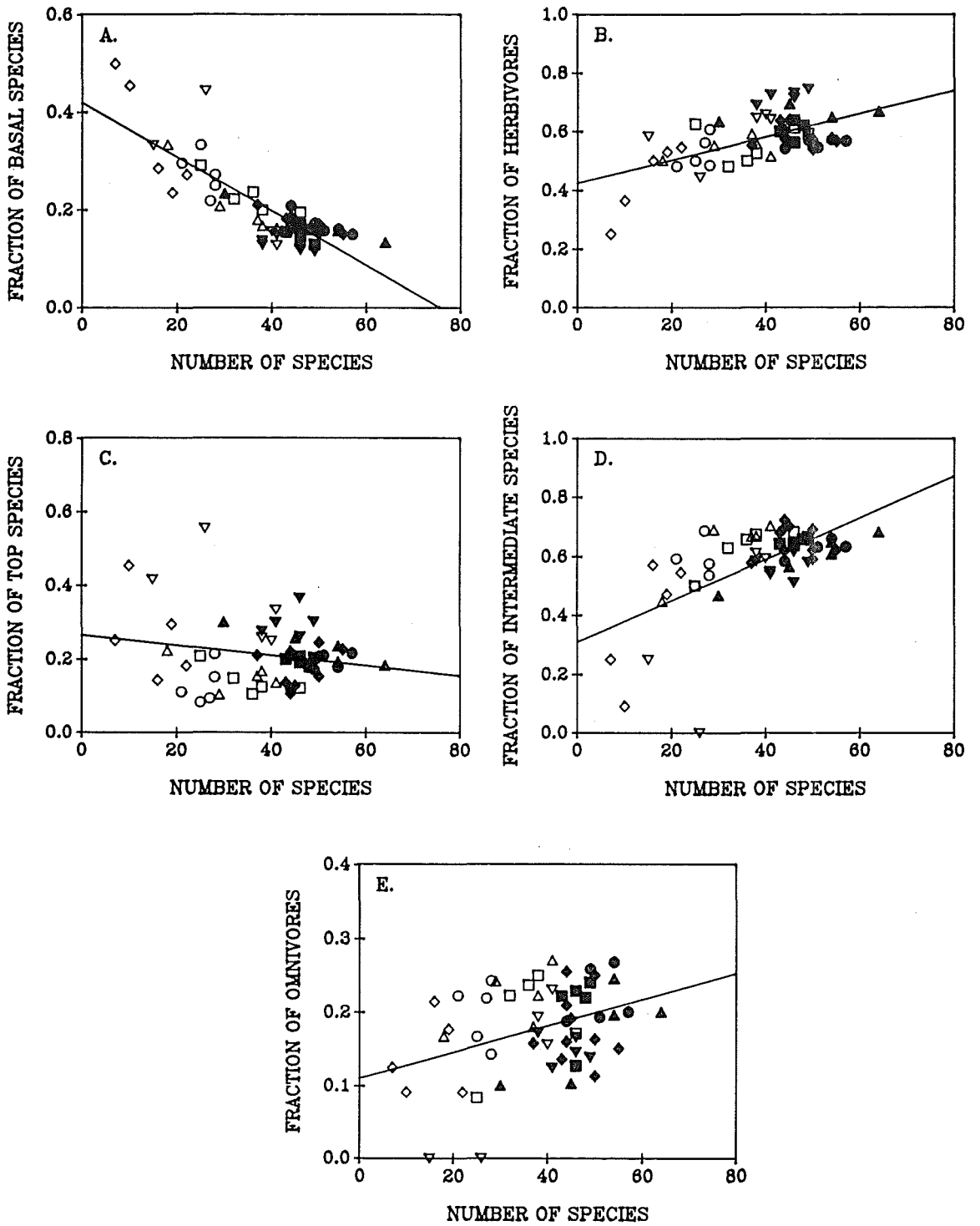


Figure 13.2. Fraction of basal species (A), herbivores (B), top species (C), intermediate species (D) and omnivores (E) as a function of the total number of species. Regression analyses for these relationships are given in Table 13.4. Stable sites have solid symbols: Porter River (●), Slip Spring (◆), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

Table 13.4. Results of regression analysis of the fraction of each of five trophic categories against total number of species and overall (multivariate) stability. Significance levels are indicated by *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$.

	F value	df	P	r^2	Equation
Regression against species number					
Basal species	92.15	1,53	***	0.63	y = 0.391 - 0.005x
Herbivores	14.01	1,53	***	0.21	y = 0.467 + 0.003x
Top species	7.10	1,53	*	0.12	y = 0.298 - 0.002x
Intermed. species	53.75	1,53	***	0.50	y = 0.304 + 0.007x
Omnivores	16.64	1,53	***	0.24	y = 0.097 + 0.002x
Regression against overall stability					
Basal species	57.99	1,49	***	0.62	y = 0.161 + 0.098x
Herbivores	22.87	1,49	***	0.33	y = 0.652 - 0.083x
Top species	0.20	1,49	n.s.	0.08	
Intermed. species	10.46	1,49	**	0.34	y = 0.579 - 0.092x
Omnivores	0.59	1,49	n.s.	0.32	

(Fig. 13.10) as stability decreased ($F = 28.26$, $df = 1,49$, $P < 0.05$, $r^2 = 0.48$).

The regression of number of predator species as a function of prey species (Fig. 13.11) was significant using the criteria of either Cohen (1977, 1978) or Jeffries & Lawton (1985) ($F = 1304.26$, $df = 1,53$, $P < 0.05$, $r^2 = 0.96$ and $F = 84.00$, $df = 1,53$, $P < 0.05$, $r^2 = 0.61$, respectively). Both predator/prey ratios also showed a significant decrease (Fig. 13.12) with a decrease in stability ($F = 43.45$, $df = 1,49$, $P < 0.05$, $r^2 = 0.61$ and $F = 17.30$, $df = 1,49$, $P < 0.05$, $r^2 = 0.44$).

Principal components analysis of the main food web characteristics (these included average, maximum and modal food chain length, fraction of top, intermediate and basal links, complexity (number of species x connectance), fractions of each of the five principal trophic categories, and Cohen's predator/prey ratio (following the categories used by Briand (1985)) produced three principal axes that accounted for 72.08% (axis 1), 11.86% (axis 2) and 7.33% (axis 3) of the variation in the data. Axis 1 is plotted against axis 2 in Fig. 13.13. Correlations of each of these axes with 26 physical, biological, chemical and stability characteristics are listed in Table 13.7. Axis 1 was positively correlated with several stability parameters and negatively correlated with epilithic carbon concentration. Stepwise regression analysis (Table 13.8) consequently yielded spot stone movement measures and epilithic carbon concentration as important predictors of this axis

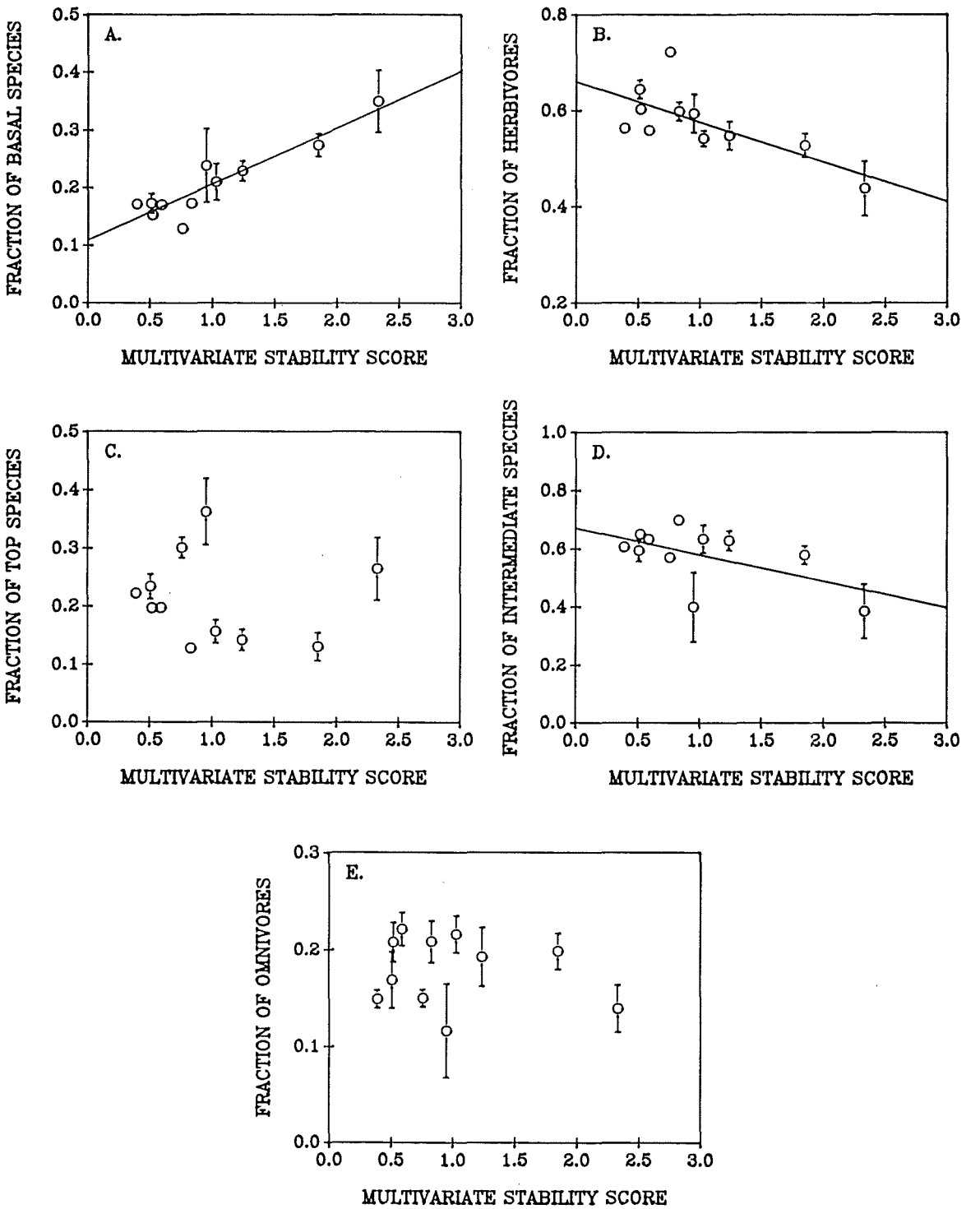


Figure 13.3. Fraction of basal species (A), herbivores (B), top species (C), intermediate species (D) and omnivores (E) as a function of overall (multivariate) stability. Plotted values are averages for each of the seasonal measures ± 1 SE. Regression analysis was performed including seasonal comparisons, the results of which are given in Table 13.4.

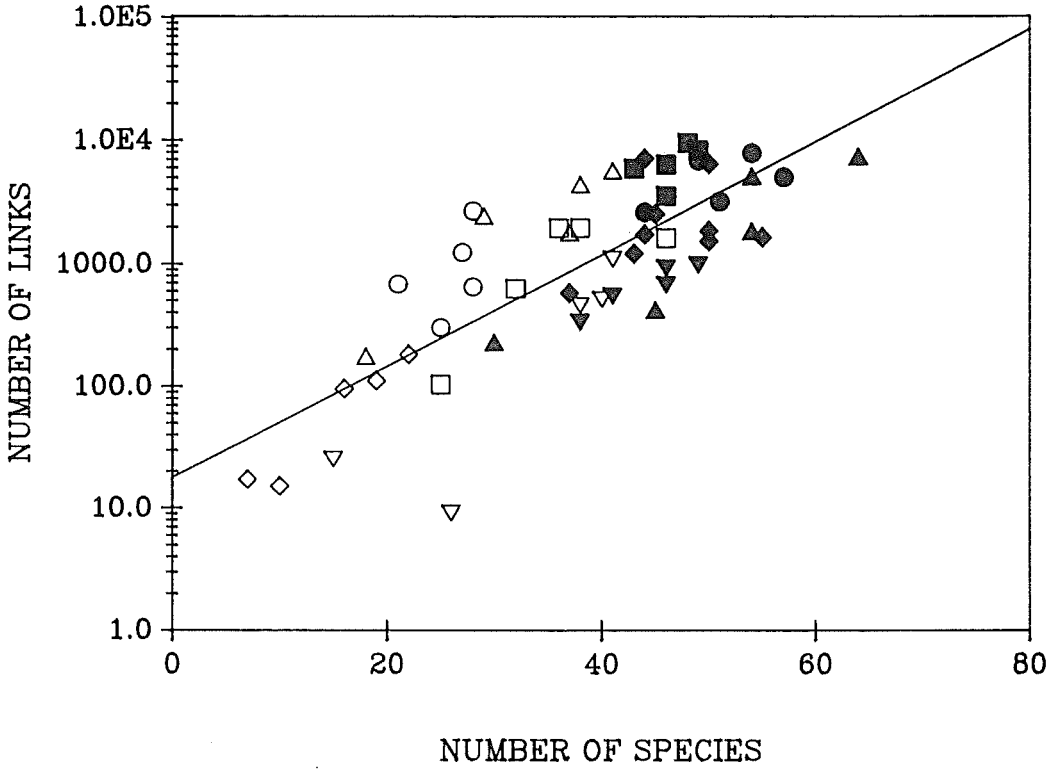


Figure 13.4. Number of trophic links as a function of total species number. Log_{10} (number of links) = 1.23 + 0.05(species number), r^2 = 0.77. Stable sites have solid symbols: Porter River (●), Slip Spring (◆), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

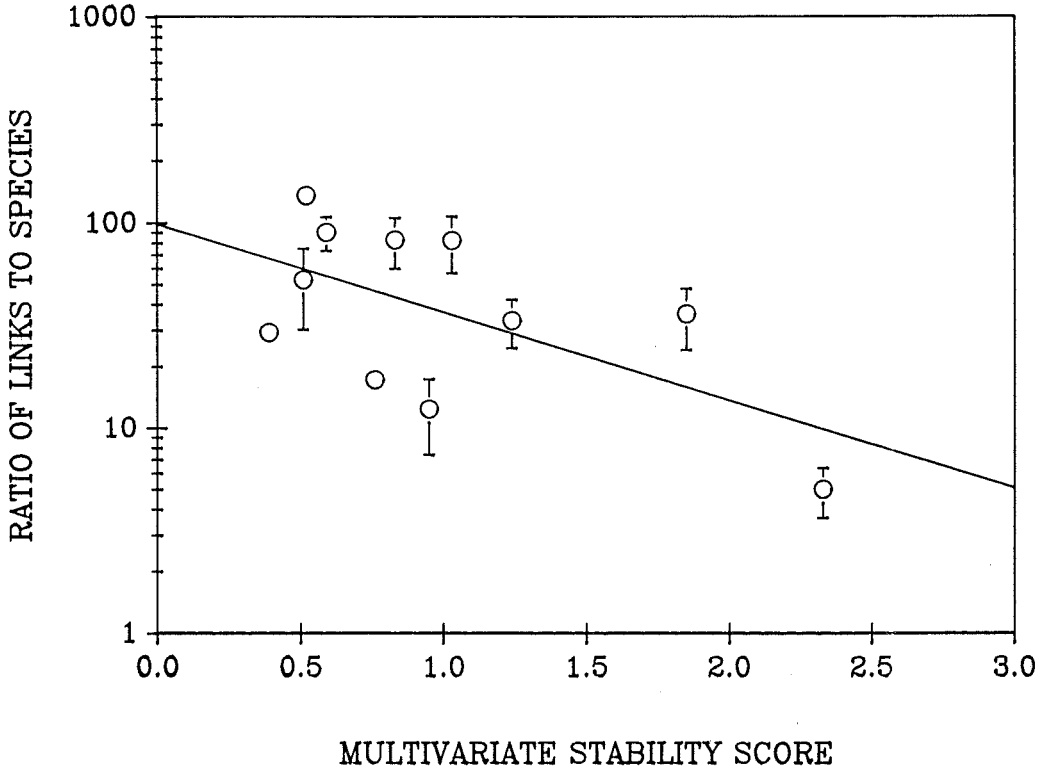


Figure 13.5. Ratio of number of links to species number, as a function of overall stability. Plotted values are averages for the seasonal ratios ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, log_{10}(ratio) = 1.50 - 0.45(stability score), r^2 = 0.43.

Table 13.5. Average, coefficient of variation and range (in parentheses) for the proportion of top-basal, top-intermediate, intermediate-intermediate and intermediate-basal trophic links in food webs collected at my study sites between October 1987 and October 1988.

Sites	Proportion of links			
	Top-Basal	Top-Intermed.	Intermed.-Intermed.	Intermed.-Basal
UNSTABLE SITES				
Kowai River	0.009	0.339	0.313	0.339
	80.40	10.15	24.04	10.15
	(0.003-0.02)	(0.29-0.38)	(0.21-0.42)	(0.29-0.38)
Whitewater Stream	0.009	0.298	0.396	0.298
	155.33	17.65	30.08	17.65
	(0.001-0.03)	(0.25-0.38)	(0.20-0.49)	(0.25-0.38)
Dry Stream	0.019	0.350	0.281	0.350
	169.37	18.06	56.65	18.06
	(0.003-0.08)	(0.31-0.46)	(0.00-0.37)	(0.31-0.46)
Craigieburn Cutting Stream	0.285	0.276	0.162	0.276
	149.36	56.16	91.39	56.16
	(0.02-1.00)	(0.00-0.36)	(0.00-0.28)	(0.00-0.36)
Bruce Stream	0.123	0.404	0.069	0.404
	156.24	19.87	99.03	19.87
	(0.01-0.47)	(0.27-0.47)	(0.00-0.14)	(0.27-0.47)
STABLE SITES				
Porter River	0.003	0.309	0.380	0.309
	54.44	8.56	14.24	8.56
	(0.001-0.01)	(0.28-0.34)	(0.31-0.44)	(0.28-0.34)
Slip Spring	0.007	0.357	0.278	0.357
	52.76	3.29	9.37	3.29
	(0.004-0.01)	(0.35-0.37)	(0.24-0.30)	(0.35-0.37)
Cora Lynn Stream	0.019	0.358	0.265	0.358
	122.78	22.42	68.02	22.42
	(0.002-0.06)	(0.27-0.44)	(0.06-0.46)	(0.27-0.44)
Middle Bush Stream	0.030	0.344	0.282	0.344
	26.93	3.48	7.41	3.48
	(0.02-0.04)	(0.33-0.36)	(0.26-0.31)	(0.33-0.36)
Grasmere Stream	0.002	0.285	0.428	0.285
	68.71	10.24	13.97	10.24
	(0.001-0.004)	(0.26-0.33)	(0.34-0.49)	(0.26-0.33)
Lake Grasmere	0.002	0.238	0.522	0.238
	48.36	6.05	5.63	6.05
	(0.001-0.003)	(0.22-0.26)	(0.48-0.56)	(0.22-0.26)

with a total r^2 of 0.53. Stepwise regression analysis of these variables with axis 2 yielded current variation, mean depth (both negative relationships) and stone associated particulate organic matter (POM) (a positive relationship) as the strongest predictors of axis 2 scores. This axis seems to represent a separation of the forest sites from the rest, as these streams were relatively small and had large amounts of POM amongst the substrate.

I also performed this analysis using each of the component link types (i.e., top-

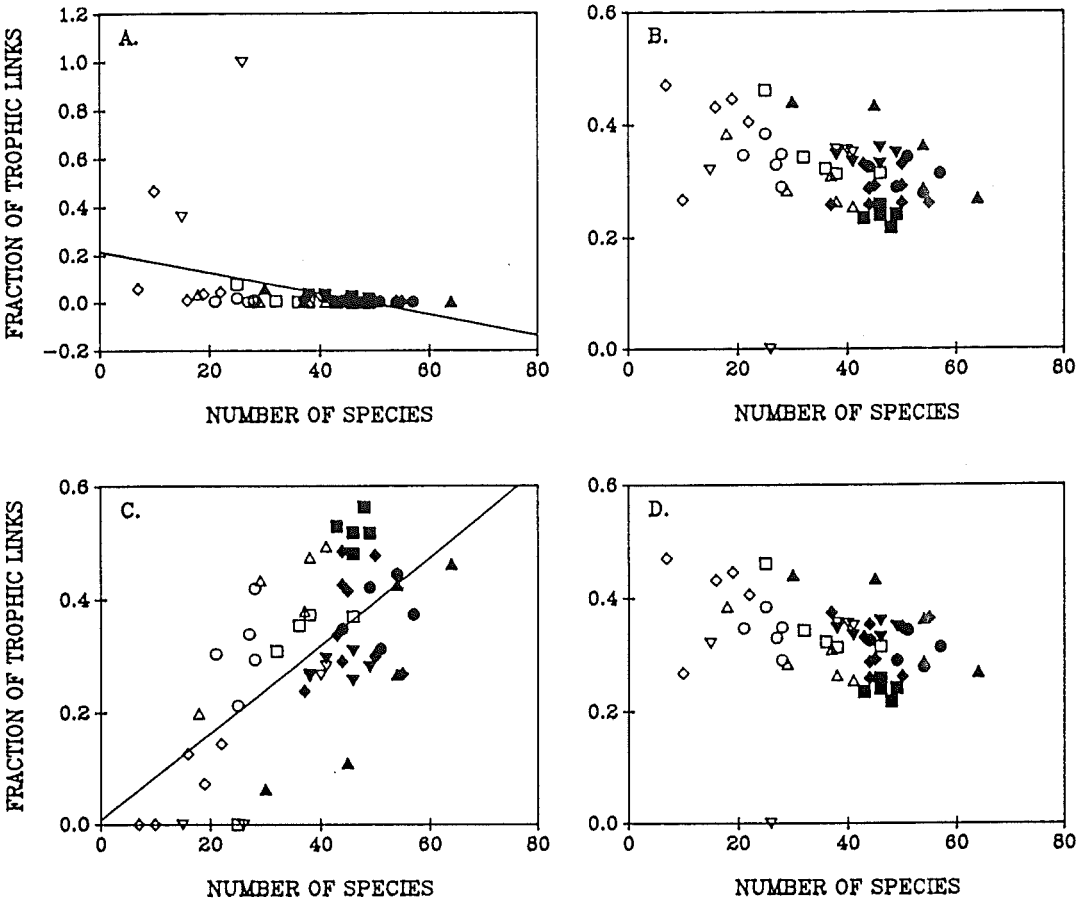


Figure 13.6. Fraction of top-basal (A), top-intermediate (B), intermediate-intermediate (C) and intermediate-basal (D) trophic links as a function of total species number. The regression analyses for these relationships are given in Table 13.6. Stable sites have solid symbols: Porter River (●), Slip Spring (◆), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◈) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

Table 13.6. Results of regression analysis of the fraction of different trophic links against total number of species and overall (multivariate) stability. Significance levels are indicated by *** $P <$ 0.001, ** $P < 0.01$, * $P < 0.05$, n.s. $P > 0.05$.

Links	*F* value	*df*	*P*	r^2	Equation
Regression against species number					
Top-Basal	17.52	1,53	***	0.25	y = 0.254 - 0.005x
Top-Intermediate	2.97	1,53	n.s.	0.05	
Intermed.-Inter.	60.52	1,53	***	0.53	y = 0.008x
Intermed.-Basal	2.97	1,53	n.s.	0.05	
Regression against overall stability					
Top-Basal	8.74	1,49	**	0.33	$y = 0.415 \log_{10}(x) - 1.959$
Top-Intermediate	5.02	1,49	*	0.13	y = 0.313 + 0.038x
Intermed.-Inter.	15.07	1,49	***	0.37	y = 0.315 - 0.114x
Intermed.-Basal	5.02	1,49	*	0.13	y = 0.313 + 0.038x

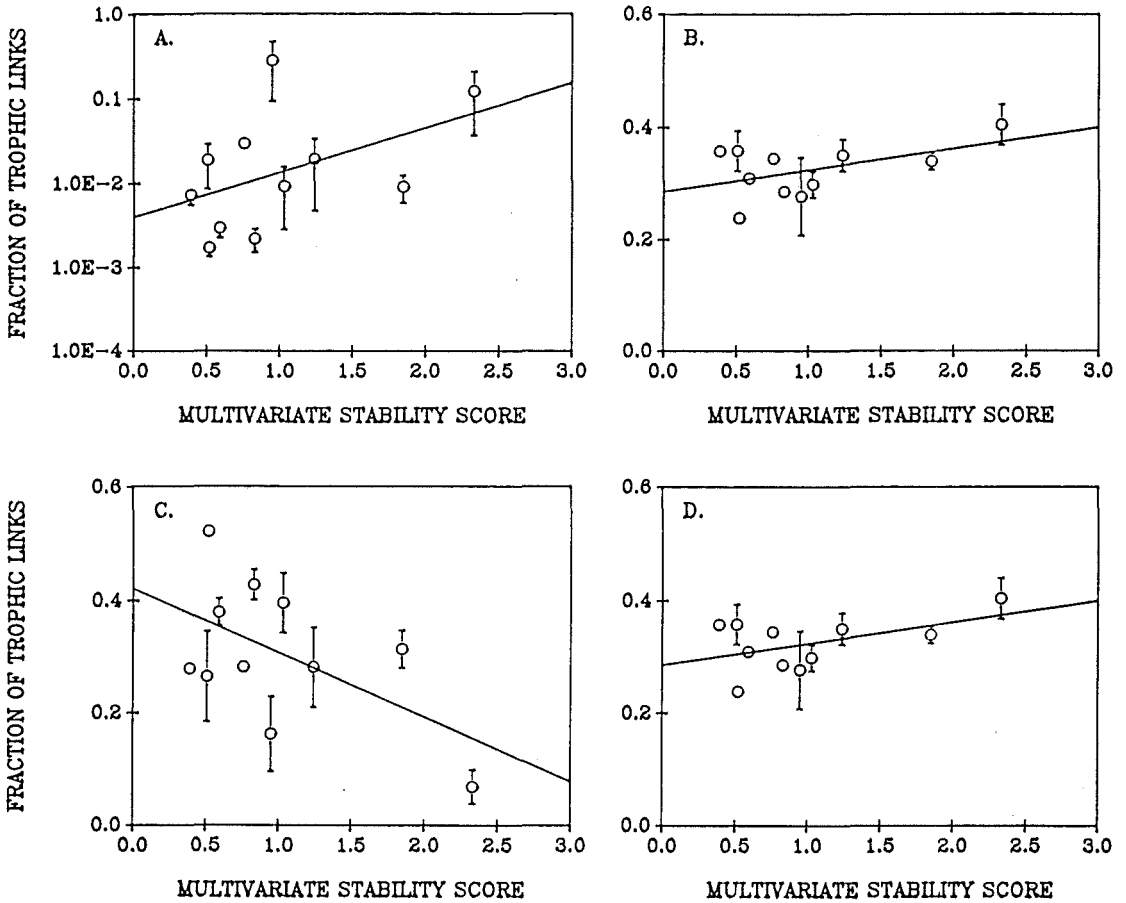


Figure 13.7. Fraction of top-basal (A), top-intermediate (B), intermediate-intermediate (C) and intermediate-basal (D) trophic links as a function of overall stability. Plotted values are averages for each of the seasonal measures ± 1 SE. Regression analyses were performed including seasonal comparisons, the results of which are given in Table 13.6.

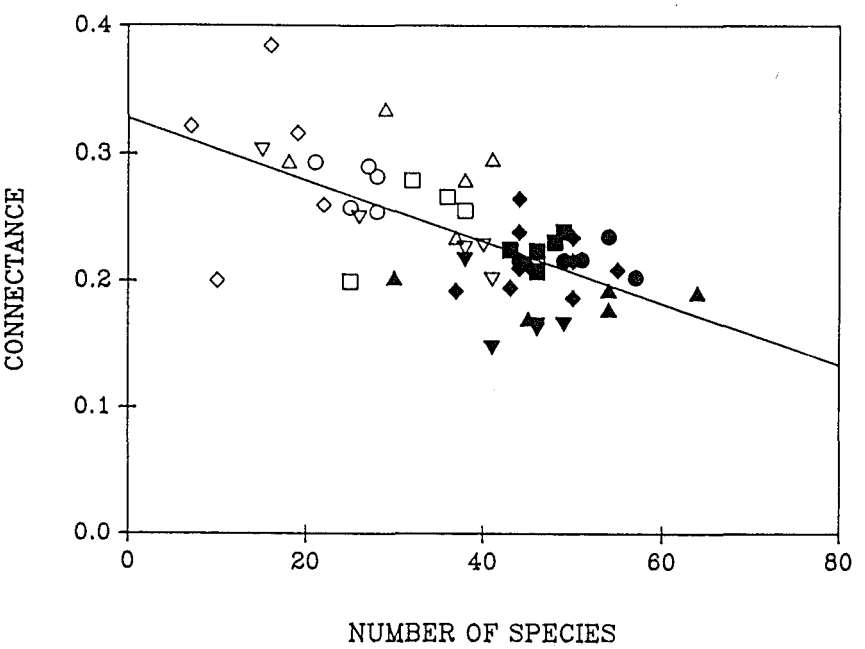


Figure 13.8. Connectance plotted as a function of total number of species. Connectance = 0.31 - 0.002(species number), r^2 = 0.32. Stable sites have solid symbols: Porter River (●), Slip Spring (◆), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

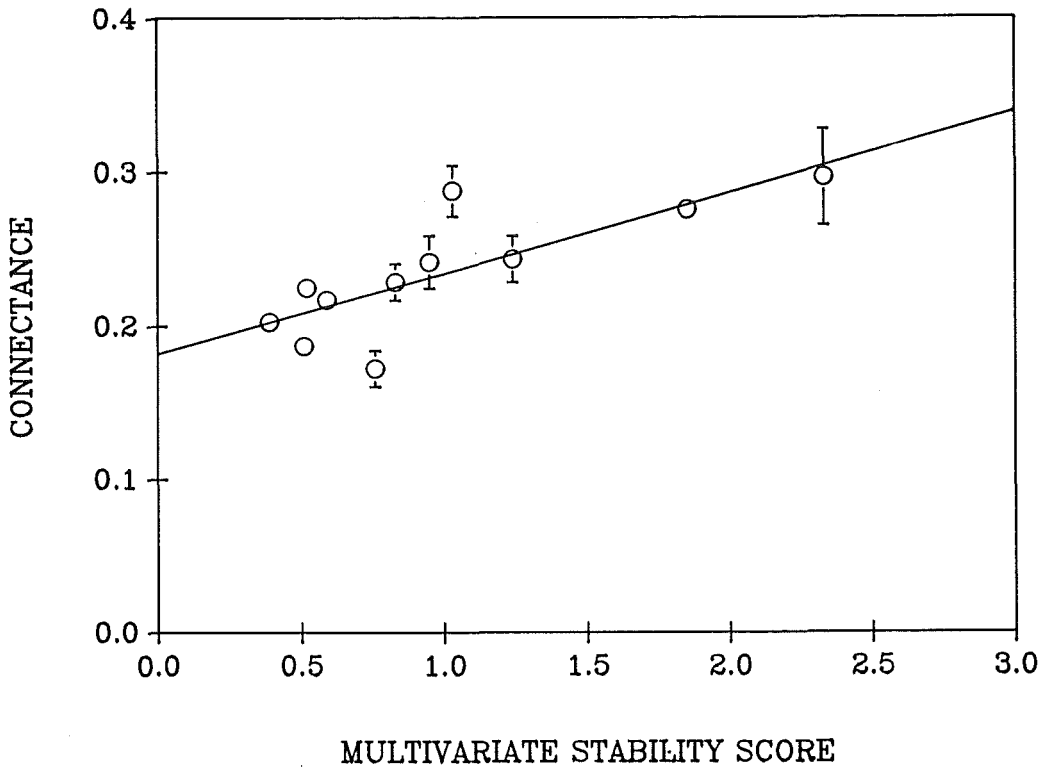


Figure 13.9. Connectance as a function of overall stability. Plotted values are averages for each of the seasonal measures ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, connectance = 0.17 + 0.05(stability), r^2 = 0.42.

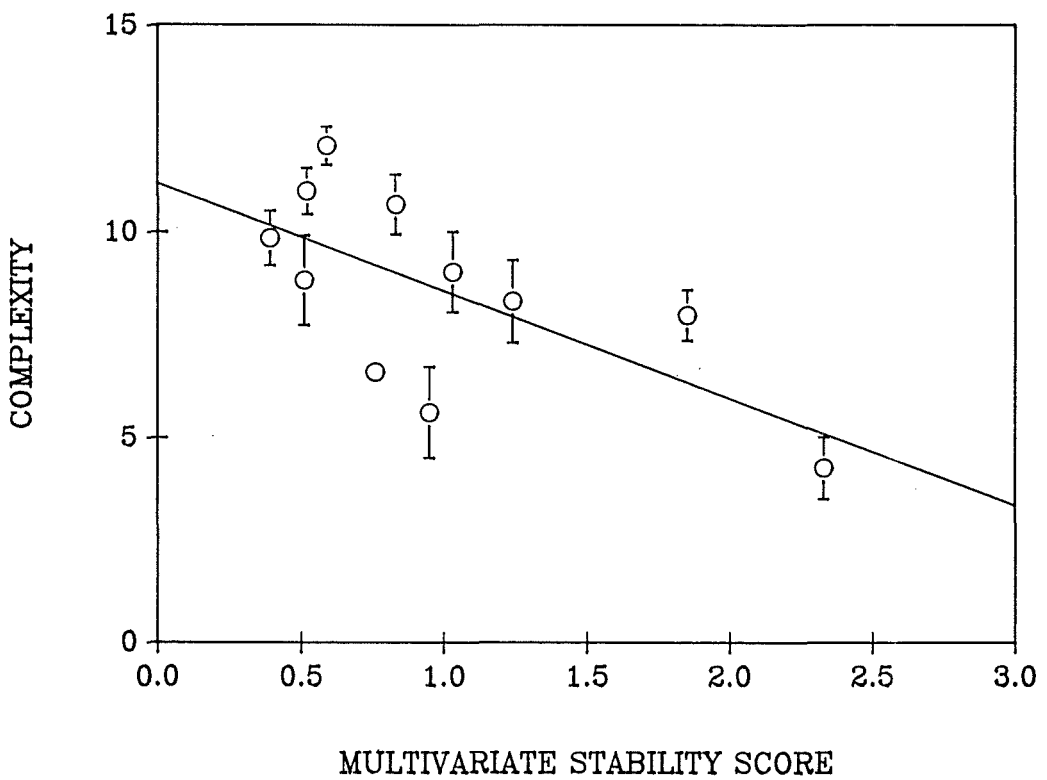


Figure 13.10. Complexity (connectance x species number) as a function of overall stability. Plotted values are averages for each of the seasonal measures ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, complexity = 9.25 - 2.62(stability), r^2 = 0.48.

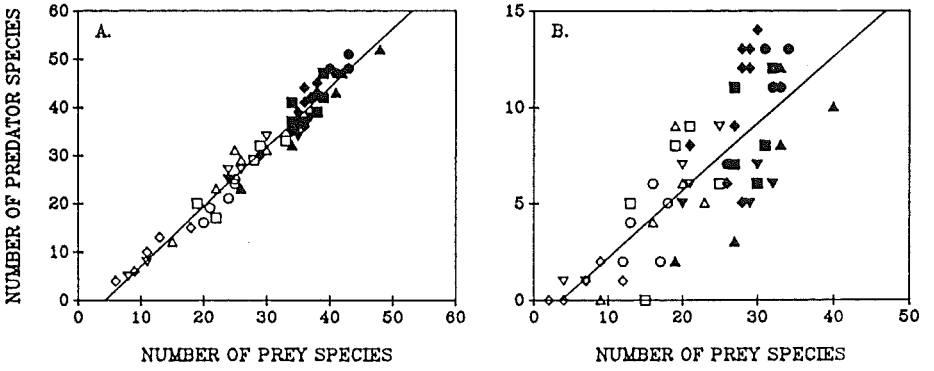


Figure 13.11. Number of predator species (as defined by Cohen (1977, 1978) (A) and Jeffries & Lawton (1985) (B)) as a function of the number of prey species. Equation A: predator species number = 1.23(prey species number) - 5.30, r^2 = 0.96; equation B: predator species number = 0.35(prey species number) - 1.27, r^2 = 0.61. Stable sites have solid symbols: Porter River (●), Slip Spring (◆), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

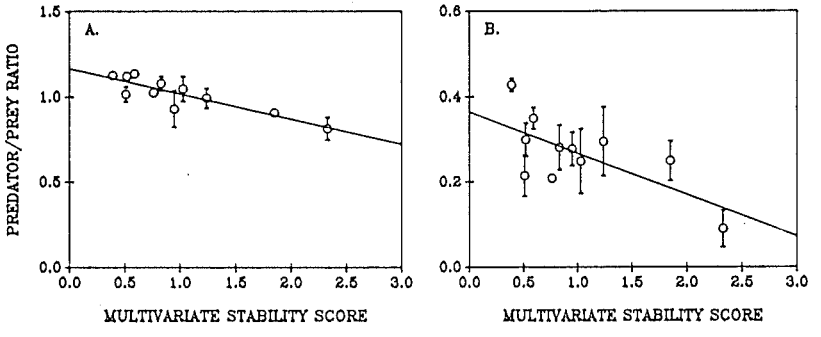


Figure 13.12. Ratio of number of predator species to prey species (as defined by Cohen (1977, 1978) (A) and Jeffries & Lawton (1985) (B)), as a function of overall stability. Plotted values are averages for each of the seasonal measures ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equations A: ratio = 1.05 - 0.15(stability score), r^2 = 0.61, B: ratio = 0.26 - 0.10(stability score), r^2 = 0.44.

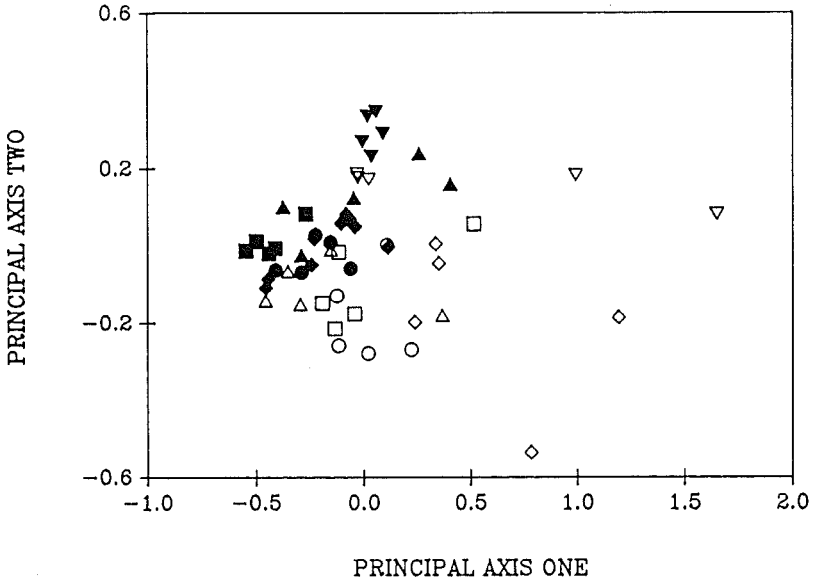


Figure 13.13. Principal axis two as a function of principal axis one for the combined food web characteristics. Stable sites have solid symbols: Porter River (●), Slip Spring (◆), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆) and Lake Grasmere (□). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

Table 13.7. Correlation (r) of principal axes one, two and three, from the principal components analysis of a number of food web characteristics, with a variety of biological, hydrological and chemical parameters. * indicates significant correlations at $P = 0.05$.

Physicochemical/ Biological parameter	Axis one	Axis two	Axis three
BIOLOGICAL			
Epilithic pigment conc.	-0.34*	0.15	0.22
Epilithic carbon conc.	-0.55*	0.10	0.37*
Coarse POM	-0.02	0.34*	-0.17
Fine POM	0.14	0.11	-0.02
Total POM	0.02	0.35*	-0.16
Stone POM	-0.14	0.61*	0.16
CHEMICAL			
Spot conductivity	-0.21	0.08	-0.12
Spot pH	-0.27*	0.10	0.17
Mean Conductivity	-0.08	0.39*	-0.05
Mean pH	-0.33*	0.08	0.10
Mean alkalinity	-0.17	0.41*	0.02
PHYSICAL			
Spot current velocity	0.30*	-0.27*	-0.27*
Spot depth	0.09	-0.37*	0.06
Spot temperature	-0.37*	-0.11	0.21
Mean current velocity	0.13	-0.55*	-0.28*
Mean depth	-0.08	-0.61*	0.08
Mean temperature	-0.36*	-0.43*	0.14
STABILITY			
Spot temperature range	-0.03	-0.34*	-0.09
Mean temperature range	0.08	-0.48*	-0.10
Current variation	0.25	-0.65*	-0.38*
Depth variation	0.34*	-0.55*	-0.15
Spot stone movement	0.57*	-0.48*	-0.07
Mean stone movement	0.47*	-0.53*	-0.24
Pfankuch bottom component	0.51*	-0.30*	-0.30*
Tractive force	0.46*	0.14	-0.32*
Overall stability	0.43*	-0.57*	-0.30*

basal, top-intermediate) instead of the broader groupings of top, intermediate and basal link types. A plot of axis 2 against axis 1 is given in Fig. 13.14. Axis 1 showed a similar pattern to that in the analysis above such that stability and epilithic carbon concentration decreased as the axis scores increased. However, axis

Table 13.8. Stepwise regression results for principal axes one, two and three from the principal components analysis of food web structure, against 26 biological, physicochemical and stability measurements. Variables were added and removed from the model at a probability level of 0.05.

	Variable entered	Parameter estimate	Partial r^2	Model r^2
PRINCIPAL AXIS ONE				
Intercept		0.83		
	Spot stone movement	0.01	0.33	0.33
	Mean temperature	-0.08	0.16	0.49
	Epilithic carbon conc.	-0.01	0.04	0.53
PRINCIPAL AXIS TWO				
Intercept		0.16		
	Current variability	-0.004	0.43	0.43
	Stone POM	0.01	0.13	0.56
	Mean depth	-0.01	0.07	0.63
PRINCIPAL AXIS THREE				
Intercept		0.21		
	Current variability	-0.01	0.14	0.14
	Mean depth	0.01	0.09	0.23
	Mean alkalinity	-0.01	0.07	0.30

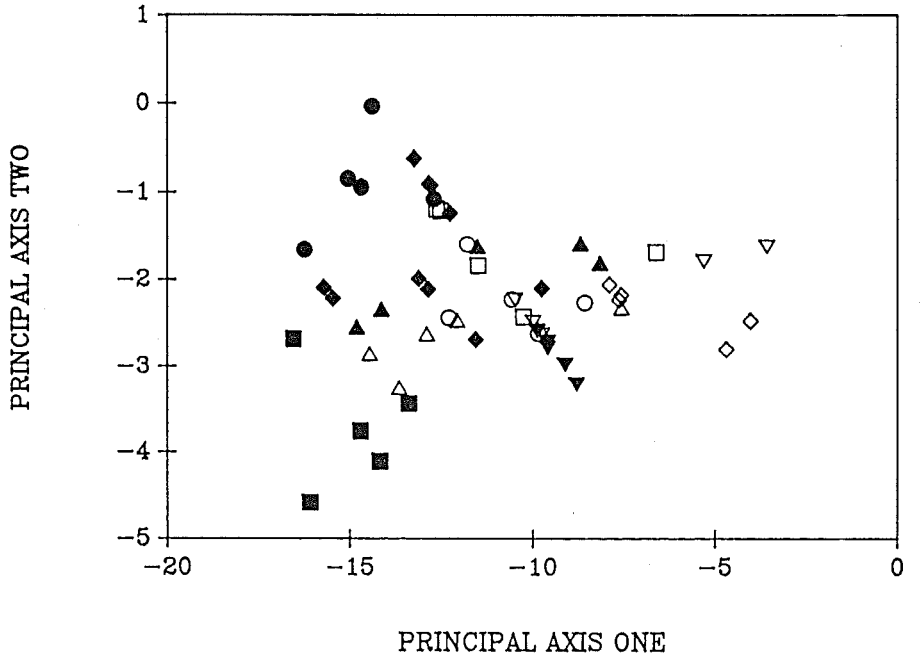


Figure 13.14. Principal axis two as a function of principal axis one for the combined food web characteristics, but with trophic link categories top, basal and intermediate replaced by specific link types (e.g. top-basal, top-intermediate). Stable sites have solid symbols: Porter River (●), Slip Spring (◆), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

2 seemed to represent a gradation from the Lake shore food webs to the stable stream food webs.

Functional Feeding Group Characteristics

The mean relative abundance of functional feeding groups at each of the sites is plotted in Fig. 13.15. All sites were strongly dominated by collector/browsers (60-90%). Principal components axes 1 and 2 for number of species, total numbers of invertebrates and relative abundance of each of these functional feeding groups is plotted in Fig. 13.16, and the variables evaluated as the best predictors of these axes by stepwise regression analysis are listed in Table 13.9. For both species number and total numbers, axis 1 seemed to correspond to stability and/or epilithic biomass (both variables are closely linked). However, this is probably more indicative of the fact that overall, species number and total numbers decreased as stability and/or epilithic biomass decreased, not that there was any trend in functional feeding categories with these variables.

This is borne out by the analysis of the relative abundances of each of these categories (Fig. 13.16) which yielded no clear patterns except that the two forest sites were separated from the rest. Both these sites had proportionally more predators and filterers (principally Ostracoda).

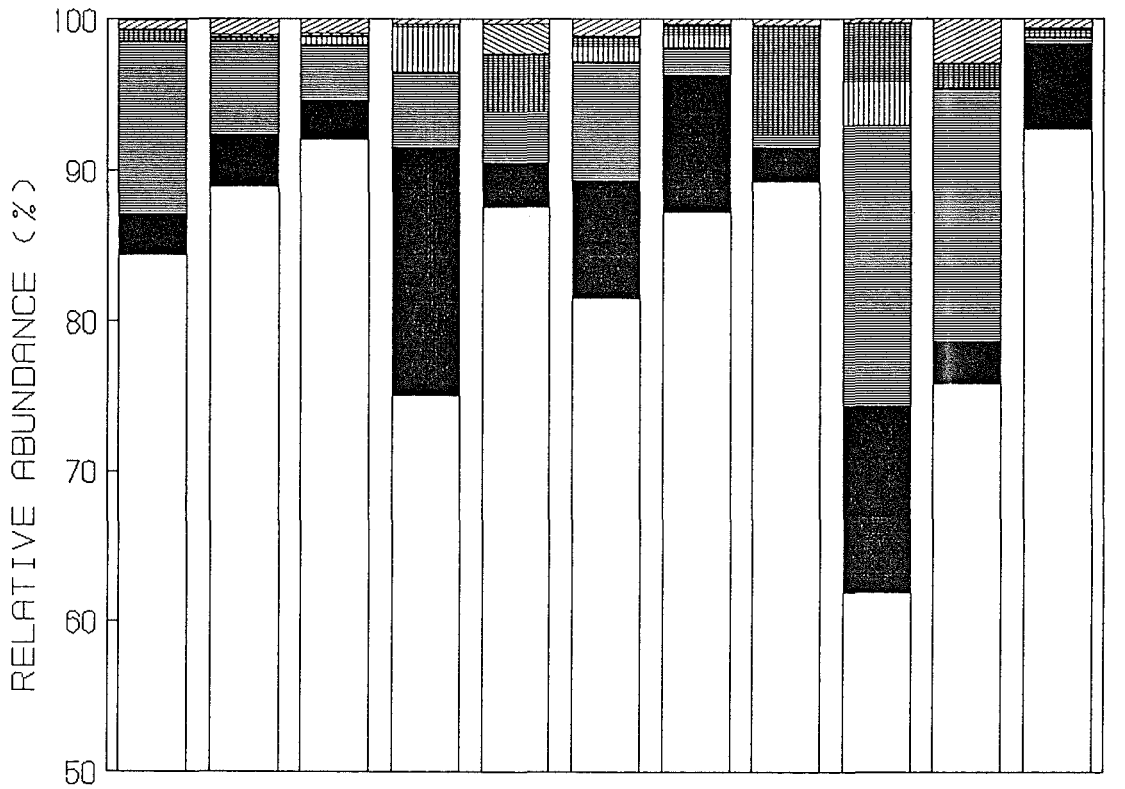


Figure 13.15. Mean relative abundances of the functional feeding categories at each of the study sites. Collector/browsers (□), predators (■), filterers (▤), shredders (▥), piercers (▥), parasites (▨) and non feeding groups (▨).

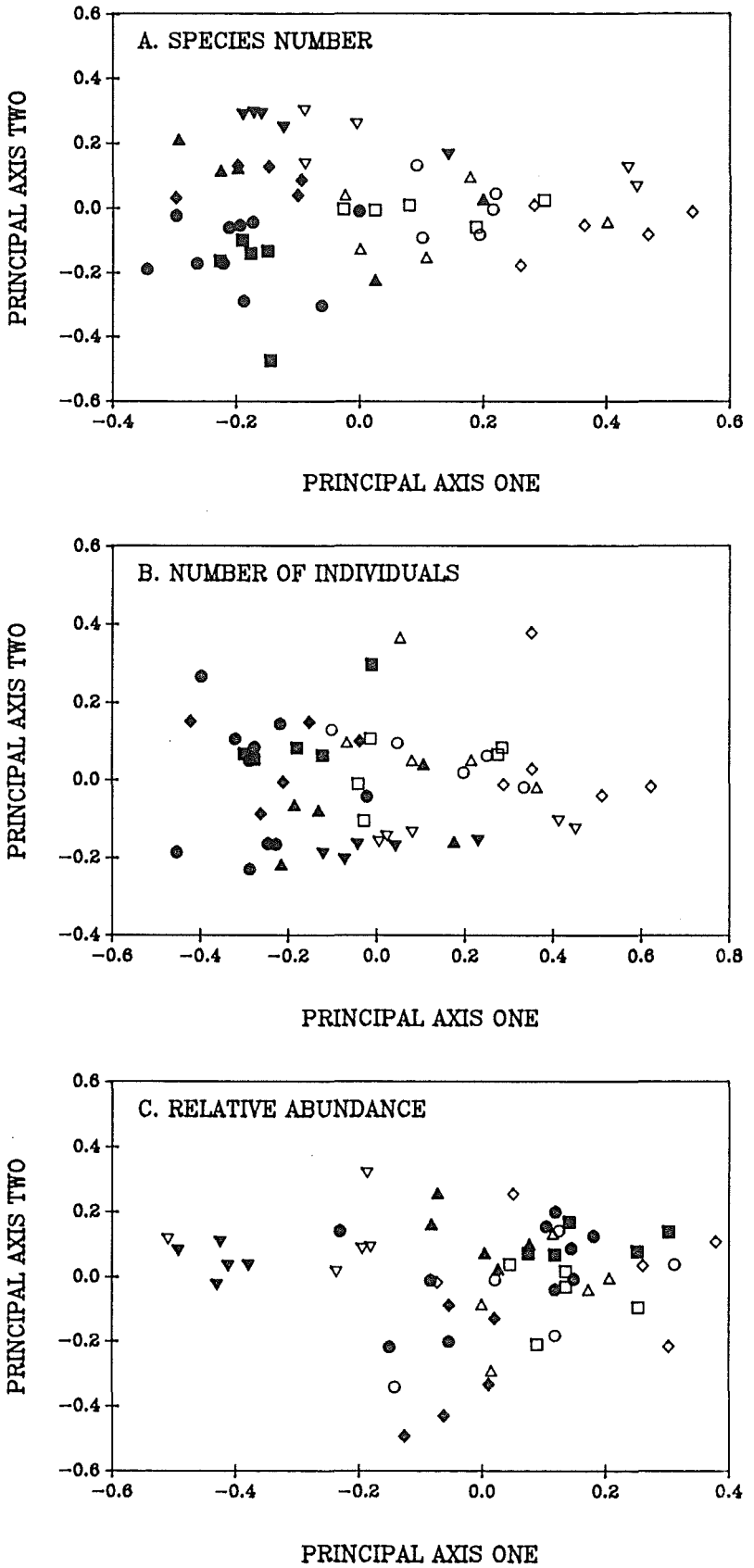


Figure 13.16. Principal axis two as a function of principal axis one for species number, total numbers and relative abundances of each of the six functional feeding categories. Stable sites have solid symbols: Porter River (●), Slip Spring (◆), Cora Lynn Stream (▲), Middle Bush Stream (▼), Grasmere Stream (◆) and Lake Grasmere (■). Unstable sites have open symbols: Kowai River (○), Whitewater Stream (△), Dry Stream (□), Craigieburn Cutting Stream (▽) and Bruce Stream (◇).

Table 13.9. Stepwise regression results for principal axes one, two and three for number of species, total number of invertebrates and relative abundance of each of the six functional feeding groups against 26 biological, physicochemical and stability measurements. Variables were added and removed from the model at a probability level of 0.05.

Variable entered	Variable removed	Parameter estimate	Partial r^2	Model r^2
NUMBER OF SPECIES				
PRINCIPAL AXIS ONE				
Intercept		0.19		
Spot stone movement		0.002	0.54	0.54
Epilithic carbon conc.		-0.01	0.14	0.68
Stone POM		-0.01	0.05	0.73
Epilithic pigment conc.		-0.01	0.02	0.75
Spot conductivity		-0.001	0.02	0.78
PRINCIPAL AXIS TWO				
Intercept		0.08		
Epilithic pigment conc.		-0.02	0.26	0.26
Mean depth			0.16	0.42
Mean alkalinity		0.01	0.07	0.49
Pfankuch bottom component		0.03	0.06	0.55
Overall stability		-0.35	0.11	0.66
	Mean depth		0.001	0.65
Mean pH		-0.15	0.03	0.69
PRINCIPAL AXIS THREE				
Intercept		0.08		
Mean depth		-0.004	0.10	0.10
NUMBER OF INDIVIDUALS				
PRINCIPAL AXIS ONE				
Intercept		0.28		
Epilithic carbon conc.		-0.01	0.54	0.54
Spot stone movement		0.002	0.18	0.72
Mean current velocity		-0.01	0.04	0.76
Epilithic pigment conc.		-0.02	0.05	0.81
Stone POM		-0.01	0.03	0.84
Spot current velocity		0.23	0.02	0.86
Mean stone movement		0.002	0.02	0.88

Table 13.9 (*Continued on following page*)

Table 13.9. (*Continued*)

PRINCIPAL AXIS TWO			
Intercept	0.59		
Mean depth	0.01	0.22	0.22
Tractive force	-0.002	0.07	0.29
Spot pH	-0.08	0.07	0.36
PRINCIPAL AXIS THREE			
Intercept	-0.33		
Mean temperature	0.04	0.21	0.21
Epilithic pigment conc.	-0.01	0.10	0.31
RELATIVE ABUNDANCE			
PRINCIPAL AXIS ONE			
Intercept	-0.09		
Stone POM	-0.02	0.28	0.28
Epilithic pigment conc.	0.03	0.11	0.39
Depth variability	0.02	0.11	0.50
PRINCIPAL AXIS TWO			
Intercept	0.36		
Mean current velocity	-0.004	0.20	0.20
Spot stone movement	0.003	0.18	0.38
Mean temperature range	-0.02	0.12	0.51
Spot conductivity	-0.001	0.04	0.55
PRINCIPAL AXIS THREE			
Intercept	1.73		
Mean pH	-0.23	0.24	0.24
Tractive force	0.002	0.10	0.33
Fine POM	-0.28	0.07	0.40
Mean depth	-0.004	0.05	0.45

There has been considerable interest recently in the relative impact of predators on stream communities , with respect to the stability of stream environments, stimulated by Peckarsky's harsh-benign hypothesis (Peckarsky, 1983). I therefore also examined how predator numbers and relative abundance (predator species number is considered above) changed with the stability of the stream. Results are plotted against overall stability in Fig. 13.17. Total number of predators declined significantly as stability decreased (F = 132.25, df = 1,49, $P < 0.05$, r^2 = 0.77). However, this simply reflected a general decline in densities as the relative abundance of predators showed no trend as stability declined (F = 3.84, df = 1,49, $P > 0.05$, r^2 = 0.15).

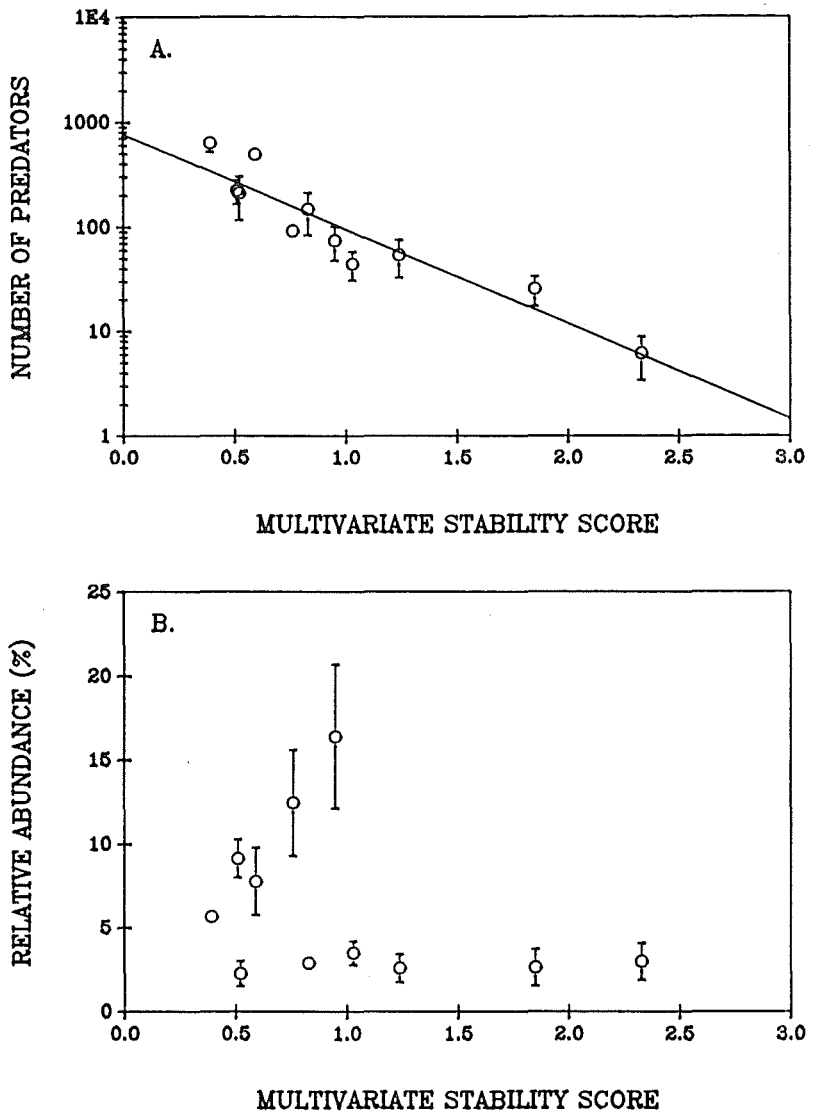


Figure 13.17. Total number of predators (A) and relative abundance of predators (B) as a function of overall stability. Plotted values are averages for each of the seasonal measures ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equation, $\log_{10}$(total number of predators) = 2.44 - 0.93(stability score), r^2 = 0.77.

DISCUSSION

How then do the characteristics of these food webs compare with the patterns determined from the 113 food webs compiled from the literature? Modal food chain length, as in the compiled webs (Elton, 1927; Hutchinson, 1959; Pimm & Lawton, 1977; Pimm, 1982), was short with a range between two and six species (the published chains were typically three or four species long). The length of these chains exhibited a significant decrease as the stability of the site decreased. Briand & Cohen (1987) also found shorter chains in less stable habitats, although they were unable to convincingly factor out the influence of habitat dimension from their analysis. Kitching and Pimm in their work on "phytotelmata" commu-

nities (Kitching, 1983; Kitching & Pimm, 1985; Pimm & Kitching, 1987) also offer some supporting evidence that shorter food chains occur in less stable habitats. Thus, Kitching (1983) found that food chains were longer in Australian than in English tree holes, where leaf inputs were more constant and climatic fluctuations were less severe. Similarly, Kitching & Pimm (1985) concluded that "spatial and temporal uncertainty" were the major determinants of food chain length in a world-wide range of "phytotelmata" communities. In an experimental disturbance of tree hole communities in Queensland they also found that species feeding higher in the food chains colonised more slowly (Pimm & Kitching, 1987), indicating that disturbances may limit food chain length.

A number of explanations have been put forward to explain why food chains are typically short (Pimm, 1982; Kitching & Pimm, 1985; Lawton, 1989). The two dominant hypotheses are the energetic constraints and the dynamic constraints hypotheses. The energetic constraints hypothesis predicts that chains will typically be short because of inefficient transfer of energy between links (Hutchinson, 1959) such that an organism at say the 20th trophic level would theoretically require an entire continent to support it (Slobodkin, 1961). Thus, food chains in less productive systems should be shorter. However, the evidence for and against this hypothesis is conflicting and not particularly convincing (Oksanen *et al.*, 1981; Pimm, 1982). The dynamic constraints model is based on Lotka-Volterra equations and reasons that because long food chains will have mathematically longer return times from disturbance, they are less likely to exist in the real world (Pimm & Lawton, 1977). Unstable habitats will therefore be predicted to have shorter food chains (the evidence in support of this is given above).

Another two less likely and untestable hypotheses are the size and design constraints hypothesis and evolutionary shortening (Pimm, 1982; Kitching & Pimm, 1985). The former predicts that because predators are generally larger than their prey, there are mechanical limits to the size an animal can become in order to feed higher up the chain and therefore limits to the number of possible links that can occur (Hutchinson, 1959). Evolutionary shortening predicts that because there is more energy available lower in the food chain, evolutionary pressure will be higher for animals to remain at these levels. Hastings & Conrad (1979) predicted this evolutionary pressure would lead to grazing food chains of length three.

While my results suggest support for the dynamic constraints hypothesis, in that shorter food chains are found in the less stable streams, these streams also appear to be the less productive sites (i.e., primary biomass is lower). Thus, my results could equally well support the energetic constraints model.

Although food chain lengths conformed nicely to previously observed patterns, the proportion of basal, intermediate and top species at my study sites did not, in that the fraction of each of these trophic categories changed markedly with the total number of species present in the web. Briand & Cohen (1984) and Cohen & Briand (1984), in contrast, found that the proportion of basal, intermediate and top species was constant and independent of the total number of species in 62 published food webs. The difference appears to lie primarily in the basal and intermediate species groups. The regression of the fraction of top species against total number of species is a weak one (r^2 = 0.12) and has a y-intercept of 0.298, consistent with the 0.285 recorded by Briand & Cohen (1984). The overall means for the fraction of basal species and the fraction of intermediate species are 0.206 and 0.580, respectively and are remarkably similar to that recorded by Briand & Cohen (1984) of 0.190 and 0.525, respectively. However my ratios changed markedly as the total number of species present in a web increased.

The changing relationship between species number and the proportion of each of the trophic categories, seems to lie in an interaction between the relatively constant number of basal species (despite changes in stability) and a decrease in total species number in the less stable streams. Thus the fraction of total species attributed to basal species increased with decreasing stability and the fraction of intermediate species decreased proportionately (the fraction of top species did not appear to change). This may be a consequence of coarser taxonomic discrimination at the basal level (i.e., groups such as diatoms and fungi as opposed to generic or species groups at higher levels), although for diatoms at least there did not appear to be a marked change in the number of genera as stability of the site changed (see Chapter 3). It is more likely to be a result of the generalized diets of many animals in New Zealand streams (Winterbourn *et al.*, 1984; Winterbourn, 1987), such that although stability of the stream may change, invertebrates remain predominantly collector/browsers, feeding on fine particulate organic material and diatoms.

The number of predator species (as defined by both Cohen (1977, 1978) and Jeffries & Lawton (1985)) increased linearly as the number of prey species increased. Although the slope for the "Jeffries-Lawton" relationship was slightly higher (1.14) than the value they recorded (0.75), it was very similar (1.23) to that recorded by Cohen (1.33). However, although the ratios were roughly constant they both showed a significant decrease with stability.

Cohen & Briand (1984) also found a constant proportion of each of the four categories of trophic links between basal, intermediate and top species as total number of species increases, although variation around this constant was large. I

found a constant proportion of top-intermediate and intermediate-basal links, but found a significant increase in intermediate-intermediate links and a decrease in top-basal links with increasing species number; however, both relationships showed large variations. This trend is also reflected in a decrease in intermediate-intermediate links and an increase in the other link types as stability decreased. A change in the relative proportion of trophic links with environmental stability is also in conflict with the findings of Cohen & Briand (1984) who recorded proportionately more top-basal links in constant environments. However, the overall average proportion of linkage types in my data (0.046, 0.323, 0.307, 0.323 for top-basal, top-intermediate, intermediate-intermediate and intermediate-basal, respectively) were close to those recorded by Cohen & Briand (1984) (0.077, 0.348, 0.301 and 0.274, respectively).

The total number of links in each of the food webs was proportional to the number of species as found by Cohen & Briand (1984), however, the relationship was a log linear one rather than the simple linear one they recorded. Cohen & Briand also claimed that the ratio of links to species would be higher in more constant environments, and this was borne out by my results.

Connectance showed a linear decline with increasing species number, and partially supports the hyperbolic relationship found by a number of others (Rejmanek & Stary, 1979; Yodzis, 1980; Pimm, 1982; Cohen *et al.*, 1985) although not all (Winemiller, 1989). However, connectance increased as environmental stability decreased, in direct contrast with the findings of others (Briand, 1983; Cohen *et al.*, 1985). While this may lead to instability of the community (mathematically speaking) it makes intuitive sense that the species which can survive in unstable habitats are those that have broader feeding habits. To maintain community stability in these unstable habitats (all else being equal) would necessitate weaker average interactions between species in these communities and their prey, something that seems highly likely in an unstable environment.

Given the significant changes in each of the components of these food webs with stability, it is not surprising that the principal underlying factor of overall food web structure is stability acting either directly or through its effect on the energetic base of the food web. Whether the site was open or forested also seemed to be important, although whether this was the result of a different food base or because no fish occurred at these sites is difficult to say.

Briand & Cohen (1984) and Cohen & Briand (1984) found that the food webs in constant environments were more variable than those in fluctuating environments (e.g., in the proportions of links and species at various trophic levels). However, I found no evidence for this, and in fact the reverse may have been true

depending on what particular characteristic was considered. Many of the differences between food webs in constant and fluctuating environments recorded in their studies seem more likely to have been a consequence of broad habitat differences and the effects of them on environmental variability. They suggested that differences in food webs between fluctuating and constant environments reflected greater constraints on the trophic organisation of webs in fluctuating environments. My data suggest the opposite, for example in the principal components analysis of overall food web structure (Fig. 13.13) the stable sites are all tightly grouped together, whereas the unstable sites are spread out on both axes. Similarly, connectance appeared to be greater under conditions of lower stability, indicating a structure that was more connected but where the connections may themselves have been weaker.

As with food chain lengths, a number of hypotheses have been proposed to explain observed patterns in food web structure (for reviews see Pimm, 1982; Lawton & Warren, 1988; Lawton, 1989). Of these the two principal hypotheses are the Lotka-Volterra and cascade models. The former depends on tightly coupled reciprocal dynamics between species (Pimm, 1982; May, 1979; Lawton 1989); for example, predators affect prey populations and vice versa. If webs are donor-controlled (i.e., prey populations affect predator populations but are not themselves affected by predator levels) or most links are weak, then Lotka-Volterra models will be poor predictors of food web structure (Warren, 1989). Strong interactions between aquatic invertebrates have been demonstrated (e.g., McAuliffe, 1984a; Hart, 1985; Dudley *et al.*, 1990), however, the generality of the occurrence of such relationships is far from resolved (Reice, 1985).

The other, very different explanation of food web structure, the cascade model (Cohen & Newman, 1985; Cohen *et al.*, 1985; Cohen *et al.*, 1986; Newman & Cohen, 1986), is a non-dynamic model in which species are arranged in a hierarchy such that species can feed upon those below them in the hierarchy and are themselves fed on by those above. The cascade model appears to predict a number of the reported patterns in the literature, however, the density of links per species must be fixed at observed levels before the cascade model yields the correct results (Lawton, 1989). However, why the density of links per species should be constant is not addressed by the model, although one possible mechanism leading to the type of hierarchy required by the model is an ordering of species based on body size, such that species feed only on others smaller than themselves (Warren & Lawton, 1987; Cohen & Newman, 1988). This would appear to hold for my stream communities.

The cascade model is more likely to explain food web structure in my streams

than are Lotka-Volterra models, however, I have not examined how specific predictions of either model conforms with food web patterns recorded in my study communities. Warren (1989) also concluded that the cascade model was the most appropriate model for the food web structure of his pond invertebrate communities, however, although some observed food web parameters were consistent with the predictions of the model others were not (e.g., food chain length). It may be that the patterns observed in these and other food webs are the result of a number of interacting factors and that no single explanation will prove sufficient (Lawton, 1989).

In contrast to the analysis of food web structure, investigation of invertebrate communities based on functional feeding group categories was not particularly enlightening. Habitat stability had little or no effect on feeding group structure, and the vast majority of invertebrates were collector/browsers at all these sites. This is in agreement with the picture that has emerged with respect to New Zealand stream and river invertebrate communities in general (Winterbourn *et al.*, 1984; Winterbourn, 1987; Quinn & Hickey, 1990a). Similarly, environmental stability had little effect on the relative abundance of invertebrate predators. Rather interestingly however, the two forest streams appeared to have markedly higher predator relative abundances, and it is intriguing to speculate that this was because these two sites were the only two without predatory fish.

CHAPTER 14

SYNTHESIS

The Greek philosopher Heraclitus described the dynamic nature of human life with an analogy "You cannot step twice into the same river" (Fuller, 1945). While this may be a valid description of human nature it is also an accurate description of the underlying character of lotic systems. This quote has been used several times in reviews of lotic ecology (e.g., Krumholz & Neff, 1970; Resh *et al.*, 1988) to emphasise the dynamic nature of the stream environment. Streams, probably more than most habitats, are firmly under the influence of both the surrounding environment (i.e., the catchment) and fluctuating weather patterns (Hynes, 1975; Power *et al.*, 1988). Disturbances resulting from increases in discharge can be rapid and severe, and almost all natural streams, no matter how stable, will at some stage experience increased discharge. Some streams may also suffer environmental stresses from prolonged periods of low discharge or lack of flow (as in droughts). Stream habitats also seem particularly susceptible to anthropogenic disturbances such as afforestation and chemical runoff. The open nature of stream habitats accentuates these forces so that the effects of a disturbance in the headwaters may be felt many kilometres downstream.

Disturbance is clearly a major environmental influence in many, if not all, streams (Power *et al.*, 1988; Resh *et al.*, 1988). Nevertheless, benthic communities can be both highly diverse, and at least in some circumstances, biologically structured units (e.g., Allan, 1983; Hart, 1983; Gregory, 1983; McAuliffe, 1983). Although disturbances may have severe effects on stream biotas, most effects (of natural disturbances anyway) are transitory and faunas frequently regain their pre-disturbance states within months if not weeks (Siegfried & Knight, 1977; Fisher *et al.*, 1982; Scrimgeour *et al.*, 1988) or even days (Boulton *et al.*, 1988; Doeg *et al.*, 1989). It seems that many stream invertebrates, through a combination of evolutionary and ecological processes, are able to persist in what can be a very unstable environment.

The fundamental mechanisms behind their ability to persist under such circumstances, remain essentially unknown, however. Similarly, the prevalence and circumstances under which significant interactions occur among members of stream faunas are poorly understood and any possible links between these interactions and the ability to cope with disturbances does not appear to have been considered. This is somewhat surprising considering that main-stream ecology is embroiled in a debate over how communities may be structured to cope with disturbances (May, 1981; Pimm, 1982; Kikkawa, 1986; McNaughton, 1988; Walker, 1989).

In this study, I have addressed some of these points by examining community structure in streams of differing environmental stability, but otherwise similar

physicochemical nature. Epilithic periphyton biomass was considerably higher at the more stable sites, but the taxonomic composition of these periphyton communities was more strongly influenced by riparian conditions (e.g., the light regime) than the stability of the site. Similarly, amounts of particulate organic material trapped within stream beds was determined primarily by the nature of the riparian vegetation rather than bed stability.

Invertebrate species richness and density were also markedly higher in the more stable streams. This did not appear to conform to the predictions of diversity hypotheses currently in vogue (e.g., the intermediate disturbance hypothesis (Ward & Stanford, 1983; Petraitis *et al.*, 1989) and the dynamic equilibrium model (Huston, 1979; Resh *et al.*, 1988)). However, these models appear to be very sensitive to the scale at which processes that may be controlling diversity (such as competitive exclusion and predation) are acting and whether or not there are interactions between these processes and the productivity of the stream (productivity also appeared to be linked to environmental stability). Therefore, as both the scale at which predation or competitive exclusion may be acting, and the relationship between competition and productivity are essentially unknowns the hypotheses can not be entirely discounted.

In fact, when species evenness is considered, a peak is found in streams of intermediate stability. This is also reflected in the underlying species-abundance distributions. Thus, streams of both high and low stability had distributions modelled best by the log series distribution (i.e., communities were numerically dominated by one or two species, with a large number of rare species), whereas communities at sites of intermediate stability had more even distributions of individuals amongst their constituent species, and were modelled best by the log normal distribution. Seasonal variations in these patterns were large however, although this may be the result of seasonal changes in stability associated with increased rainfall in winter.

The numerical dominance of a few species at sites of high and low stability may therefore provide some support for the above diversity hypotheses. The marked dominance of one or two species at the very stable sites may reflect their competitive superiority, such that they have eliminated other species from the majority of patches. However, species richness remained high at these sites because these other species were able to survive in one or two patches, either because microhabitat differences ameliorate competitive effects or because they continually move from patch to patch to prevent being "competitively ousted". Although it is also equally plausible that these species are numerically dominant simply because of their higher fecundity or because conditions are more to their

liking. Communities at the unstable sites were dominated by one or two species, presumably because they are better able to survive disturbance events, or because they are able to recolonise most rapidly following a disturbance (Gray, 1981a; Sagar, 1986; Scrimgeour & Winterbourn, 1989).

Community composition was dominated by members of the same "common core" of taxa reported in a number of other New Zealand studies (e.g., Rounick & Winterbourn, 1982; Graesser, 1988; Quinn & Hickey, 1990a), although their relative abundances differed markedly among sites. The taxonomic composition and relative abundance of species at a particular site seemed to be associated primarily with two factors; environmental stability and the intrinsic nature of the stream, that is, whether it was forested or open, lake shore or stream. Thus, although communities at the unstable sites had remarkably similar faunas, those at the stable sites had very different faunas which were characteristic of the particular conditions (e.g., springs, forest, grassland) at each site. Persistence of dominant taxa at all sites was relatively high, although overall it was higher at the more stable sites. In contrast, persistence of the entire fauna (both rare and common taxa) was high only at the stable sites. Similarly, seasonal variations in density and species numbers were higher at the unstable sites.

The existence and relative constancy of the dominant taxa at even the very unstable sites, could be the result of faunas either surviving disturbances (resistance) or recovering from them (resilience). Results of my experimental work and those of other studies, both experimental (e.g., Reice, 1985; Robinson & Minshall, 1986; Doeg *et al.*, 1989; Lake *et al.*, 1989) and observational (e.g., studies of flood events, Siegfried & Knight, 1977; Fisher *et al.*, 1982; Scrimgeour *et al.*, 1988), indicate that disturbances generally lead to an initial reduction in invertebrate numbers, but that they subsequently recover quite rapidly (i.e., they have high resilience).

As communities at unstable sites experience more disturbances than those at stable sites, it might be expected that the former would have a greater resilience. Communities at the unstable sites appear less complex, in that they consisted of fewer species, and therefore in line with current theory (May, 1981; Pimm, 1982; McNaughton, 1988; Walker, 1989) they might be expected to be more stable (i.e., more resilient). Their local stability (that is their ability to recover from small disturbances) was assessed by examining the eigenvalues of their community matrices. When I did this, I found that all communities had eigenvalues outside the criterion for stability, but if these eigenvalues were ignored the communities at the unstable sites had eigenvalues indicative of greater resilience. However, faunal recovery rates measured in a small-scale field experiment did not differ

between stable and unstable streams.

The finding that all the communities were unstable according to local stability criteria was unexpected, especially since faunal recovery on small substrate patches was definitely rapid. It seems likely therefore that local stability, as assessed by community matrix eigenvalues, is inappropriate in this context, either because of the very open nature of stream communities or because they are so patchily distributed. Rather, it seems that the invertebrate communities in all the study streams, irrespective of their stability, are able to recover quickly from natural disturbances (of patches of the stream bed at least). Perhaps the dynamic nature of stream habitats in general places constraints on community structure, so that all benthic communities, irrespective of stream stability at any particular point in time, have the ability to recover from disturbances when they inevitably occur.

This is not to say that these stream communities were unstructured entities, arising simply through the random accumulation of individuals, with the stable sites having more species and higher densities merely because there has been a longer time for colonisation since the last disturbance. Although the assemblages on stones at several of the unstable sites may have been the result of random colonisation by animals present in those streams, the stone assemblages at the stable sites appeared to be radically different from those that would accrue by simple accumulation of potential colonists. This interpretation was supported by the results of a similar random modelling exercise on data from a field experiment examining the effects of disturbance frequency. Differences in community structure observed between assemblages experiencing increased frequency of disturbance could not be explained by the simple accumulation of more individuals with increasing time since the last disturbance. A search for a mechanism (e.g., competition) by which the communities at the stable sites were structured (i.e., why they differ from those expected to occur by chance colonisation) was however unfruitful. An experimental study of the competitive interaction between a dominant grazer (*Potamopyrgus anitpodarum*) and the rest of the community produced equivocal results and an examination of spatial resource overlap gave no indication of any partitioning of resource usage.

Several aspects of the food webs defined in these communities were similar to those gleaned from the literature (see reviews by Lawton & Warren (1988) and Lawton (1989)). Food chain length was significantly shorter at the more unstable sites, and both predator/prey ratios and the mean proportion of trophic species (i.e., top, basal and intermediate species) and trophic links were similar to those reported in the literature (e.g., Briand & Cohen, 1984; Cohen & Briand, 1984;

Jeffries & Lawton, 1985). However, there were some notable differences, the first being that the fraction of trophic species that were basal and intermediate species declined and increased, respectively with increasing species number, whereas Briand & Cohen (1984) and Cohen & Briand (1984) found these to be constant. Secondly, connectance was higher in communities at the unstable sites whereas Briand (1983) and Cohen *et al.* (1985) found the opposite to be true, if one accepts their assessment of environmental stability. Thirdly, overall food web structure seemed more variable in the less stable streams in contrast to the conclusions of Briand & Cohen (1984) and Cohen & Briand (1984) who reported the reverse.

Some of the differences between my results and those of other studies may be attributed to the generalized diets of many animals in New Zealand streams (Winterbourn *et al.*, 1984; Winterbourn, 1987). Analysis of my communities using functional feeding groups (the trophic categories typically examined in stream invertebrate studies) revealed that between 60 and 90% of the species and individuals were collector/browsers that feed principally on epilithic algae and fine particulates.

Some of these differences may also be attributed to the fact that the studies of Briand and Cohen on the effects of environmental stability were conducted in a wide range of environments. As habitat affects food web structure in its own right (Briand, 1983, 1985; Briand & Cohen, 1987), conclusions drawn from these studies must be considered rather questionable (Lawton, 1989). Nevertheless, it is apparent from my study that when habitat differences are factored out, environmental stability has a marked effect on both overall food web structure and a number of its components (e.g., food chain length, connectance). However, whether this is primarily a consequence of environmental stability *per se* or a consequence of an associated decline in primary productivity and algal biomass with decreased stability remains unclear.

In conclusion, it is apparent that environmental stability had a marked effect on many aspects of benthic community structure in the study streams, including epilithic algal biomass, invertebrate species diversity (both richness and evenness), species-abundance patterns, persistence, and food web structure. Communities on stones in the stable streams deviated more from those expected to occur by random colonisation than did those in the unstable streams, however the reasons for this difference are still unclear. Finally, although communities in the unstable streams appeared to be less complex (and had greater theoretical resilience) they did not appear to recover more quickly than communities at the stable sites.

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REFERENCES

Abrams, P.A. (1976). Niche overlap and environmental variability. *Mathematical Biosciences* 28: 357-375.

Abrams, P.A. (1980). Some comments on measuring niche overlap. *Ecology* 61: 44-49.

Abrams, P.A. (1983). The theory of limiting similarity. *Annual Review of Ecology and Systematics* 14: 359-376.

Allan, J.D. (1975). Components of diversity. *Oecologia* 18: 359-367.

Allan, J.D. (1983). Predator-prey relationships in streams. In *Stream Ecology. Application and Testing of General Ecological Theory* (eds. J.R. Barnes & G.W. Minshall), pp. 191-229. Plenum Press, New York.

Arrhenius, O. (1922). Species and area. *Journal of Ecology* 9: 95-99.

Auerbach, M. & Shmida, A. (1987). Spatial scale and the determinants of plant species richness. *Trends in Ecology and Evolution* 2: 238-242.

Barnes, J.R. & Minshall, G.W. (1983). *Stream Ecology. Application and Testing of General Ecological Theory*. Plenum Press, New York.

Barnett, S. & Storey, C. (1970). *Matrix Methods in Stability Theory*. Thomas Nelson and Sons Ltd., London.

Bates, D.M. & Watts, D.G. (1988). *Nonlinear Regression Analysis and its Applications*. John Wiley & Sons, Inc., New York.

Bazzaz, F.A. (1975). Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology* 56: 485-488.

Beals, E.W. (1984). Bray-Curtis ordination: An effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14: 1-55.

Begon, M.; Harper, J.L. & Townsend, C.R. (1990). *Ecology: Individuals, Populations and Communities*. 2nd ed. Blackwell Scientific Publications, Oxford.

Berger, W.H. & Parker, F.L. (1970). Diversity of planktonic Foraminifera in deep sea sediments. *Science* 168: 1345-1347.

Bernstein, R.A. & Gobbel, M. (1979). Partitioning of space in communities of ants. *Journal of Animal Ecology* 48: 931-942.

Biggs, B.J.F. (1987). Periphyton. In *Aquatic Biology and Hydroelectric Power Development in New Zealand* (ed. P.R. Henriques), pp. 192-206. Oxford

University Press, Auckland, New Zealand.

Biggs, B.J.F. (1988). Algal proliferations in New Zealand's shallow stony foothills-fed rivers: Toward a predictive model. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 1405-1411.

Biggs, B.J.F. & Close, M.E. (1989). Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology* 22: 209-231.

Bishop, J.E. (1973). *Limnology of a Small Malayan River Sungai Gombak*. W. Junk, The Hague, Netherlands.

Boswell, M.T. & Patil, G.P. (1971). Chance mechanisms generating the logarithmic series distribution used in the analysis of numbers of species and individuals. In *Statistical Ecology* (eds. G.P. Patil; E.C. Pielou & W.E. Waters), pp. 99-130. Pennsylvania State University Press, University Park, PA.

Bott, T.L. (1983). Primary productivity in streams. In *Stream Ecology: Application and Testing of General Ecological Theory* (eds. J.R. Barnes & G.W. Minshall), pp. 29-53. Plenum Press, New York.

Boulton, A.J.; Spangaro, G.M. & Lake, P.S. (1988). Macroinvertebrate distribution and recolonization on stones subjected to varying degrees of disturbance: an experimental approach. *Archiv für Hydrobiologie* 113: 551-576.

Bray, J.R. & Curtis, J.T. (1957). The upland conifer-hardwood forests of northern Wisconsin. *Ecological Monographs* 22: 217-234.

Briand, F. (1983). Environmental control of food web structure. *Ecology* 64: 253-263.

Briand, F. (1985). Structural singularities of freshwater food webs. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 22: 3356-3364.

Briand, F. & Cohen, J.E. (1984). Community food webs have a scale-invariant structure. *Nature* 307: 264-267.

Briand, F. & Cohen, J.E. (1987). Environmental correlates of food chain length. *Science* 238: 956-960.

Brinkhurst, R.O. (1971). The aquatic Oligochaeta known from Australia, New Zealand, Tasmania, and the adjacent islands. *University of Queensland Papers* 3: 99-128.

Bruns, D.A. & Minshall, G.W. (1983). Macroscopic models of community organization: analyses of diversity, dominance, and stability in guilds of predaceous stream insects. In *Stream Ecology: Application and Testing of General Ecological Theory* (eds. J.R. Barnes & G.W. Minshall), pp. 231-264. Plenum Press, New York.

Bruns, D.A.; Minshall, G.W.; Hale, A.B. & La Point, T.L. (1982). Stability and organization of lotic insect communities over habitat templates along a river continuum. Idaho State University typescript.

Bunn, S.E. (1986). Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern jarrah forest, Western Australia: functional organization. *Freshwater Biology* 16: 621-632.

Bunn, S.E.; Edward, D.H. & Loneragan, N.R. (1986). Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern jarrah forest, Western Australia: community structure. *Freshwater Biology* 16: 67-92.

Burrows, C.J. (1960). Recent changes in vegetation of the Cass area, Canterbury. *New Zealand Geographer* 16: 57-70.

Burrows, C.J. (ed.) (1977). *Cass: History and Science in the Cass District, Canterbury, New Zealand.* Department of Botany Publication, University of Canterbury, Christchurch, New Zealand.

Carson, M.A. & Griffiths, G.A. (1987). Bedload transport in gravel channels. *Journal of Hydrology* (New Zealand) 26: 1-151.

Caswell, H. (1976). Community structure: a neutral model analysis. *Ecological Monographs* 46: 327-354.

Chadderton, W.L. (1990). The Ecology of Stewart Island Freshwater Communities. Unpublished M.Sc. Thesis. University of Canterbury, Christchurch, New Zealand.

Chapman, M.A. & Lewis, M.H. (1976). *An Introduction to the Freshwater Crustacea of New Zealand.* William Collins (New Zealand) Ltd., Auckland.

Chesson, P.L. (1986). Environmental variation and the coexistence of species. In *Community Ecology* (eds. J. Diamond & T.J. Case), pp. 240-256. Harper & Row, Publishers, New York.

Chesson, P.L. & Case, T.J. (1986). Overview. Nonequilbrium community theories; chance, variability, history and coexistence. In *Community Ecology* (eds.

J. Diamond & T.J. Case), pp. 229-239. Harper & Row, Publishers, New York.

Clements, F.E. (1916). Plant succession: an analysis of the development of vegetation. Carnegie Institute of Washington. Publication 242: 1-512.

Clifford, H.F. (1982). Effects of periodically disturbing a small area of substratum in a brown-water stream of Alberta, Canada. *Freshwater Invertebrate Biology* 1: 39-47.

Clifford, H.T. & Stephenson, W. (1975). *An Introduction to Numerical Classification*. Academic Press, London.

Cochran, W.G. (1950). The comparison of percentages in matched samples. *Biometrika* 37: 256-266.

Cody, M.L. (1974). *Competition and the Structure of Bird Communities*. Princeton University Press, Princeton, New Jersey.

Cody, M.L. (1989). Discussion: structure and assembly of communities. In *Perspectives in Ecological Theory* (eds. J. Roughgarden; R.M. May & S.A. Levin), pp. 227-241. Princeton University Press, Princeton, New Jersey.

Cody, M.L. & Diamond, J.M. (eds.) (1975). *The Ecology and Evolution of Communities*. Belknap Press, Cambridge, Massachusetts.

Cohen, J.E. (1977). Ratio of prey to predators in community food webs. *Nature* 270: 165-167.

Cohen, J.E. (1978). *Food Webs and Niche Space*. Princeton University Press, Princeton, New Jersey.

Cohen, J.E. & Briand, F. (1984). Trophic links of community food webs. *Proceedings of the National Academy of Sciences* USA 81: 4105-4109.

Cohen, J.E.; Briand, F. & Newman, C.M. (1986). A stochastic theory of community food webs. III. Predicted and observed lengths of food chains. *Proceedings of the Royal Society of London* B 228: 317-353.

Cohen, J.E. & Newman, C.M. (1985). A stochastic theory of community food webs. I. Models and aggregated data. *Proceedings of the Royal Society of London* B 224: 421-448.

Cohen, J.E. & Newman, C.M. (1988). Dynamic basis of food web organisation. *Ecology* 69: 1655-1664.

Cohen, J.E.; Newman, C. M. & Briand, F. (1985). A stochastic theory of

community food webs. II. Individual webs. *Proceedings of the Royal Society of London* B 224: 449-461.

Collier, K.J. (1987). Spectral properties of some West Coast waters and their relationship with dissolved organic carbon. *Mauri Ora* 14: 25-32.

Collier, K.J.; Winterbourn, M.J. & Jackson, R.J. (1989). Impacts of wetland afforestation on the distribution of benthic invertebrates in acid streams of Westland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 23: 479-490.

Colwell, R.K. & Futuyma, D.J. (1971). On the measurement of niche breadth and overlap. *Ecology* 52: 567-576.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

Connell, J.H. & Sousa, W.P. (1983). On the evidence needed to judge ecological stability or persistence. *American Naturalist* 121: 789-824.

Cook, D.R. (1983). Rheophilic and hyporheic water mites of New Zealand. *Contributions of the American Entomological Institute* 21: 1-224.

Corkum, L.D. (1989). Patterns of benthic invertebrate assemblages in rivers of northwestern North America. *Freshwater Biology* 21: 199-205.

Cowie, B. (1980). Community Dynamics of the Benthic Fauna in a West Coast Stream Ecosystem. Unpublished Ph.D. Thesis, University of Canterbury, Christchurch, New Zealand.

Cowie, B. (1985). An analysis of changes in the invertebrate community along a southern New Zealand montane stream. *Hydrobiologia* 120: 35-46.

Cowley, D.R. (1978). Studies on the larvae of New Zealand Tricoptera. *New Zealand Journal of Zoology* 5: 639-750.

Crowell, K. & Pimm, S.L. (1976). Competition and niche shifts of mice introduced onto small islands. *Oikos* 27: 251-258.

Culver, D.C. (1974). Species packing in Caribbean and North Temperate ant communities. *Ecology* 55: 974-988.

Cummins, K.W. (1962). An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *American Midland Naturalist* 67: 477-504.

Cummins, K.W. (1973). Trophic relations of aquatic insects. *Annual Review of Entomology* 18: 183-206.

Cushing, C.E. & Wolf, E.G. (1982). Organic energy budget of Rattlesnake Springs, Washington. *American Midland Naturalist* 107: 404-407.

Davies, R.W.; Wrona, F.J.; Linton, L. & Wilkialis, J. (1981). Inter- and intra-specific analyses of the food niche of two sympatric species of Erpobdellidae (Hirudinoidea) in Alberta, Canada. *Oikos* 37: 105-111.

DeAngelis, D.L. (1975). Stability and connectance in food web models. *Ecology* 56: 238-243.

DeAngelis, D.L. & Waterhouse, J.C. (1987). Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs* 57: 1-21.

Diamond, J. & Case, T.J. (1986). *Community Ecology*. Harper and Row Publishers, New York.

Doeg, T.J.; Lake, P.S. & Marchant, R. (1989). Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. *Australian Journal of Ecology* 14: 207-220.

Dudgeon, D.G. (1984). Longitudinal and temporal changes in functional organization of macroinvertebrate communities in the Lam Tseun River, Hong Kong. *Hydrobiologia* 111: 207-217.

Dudley, T.L.; D'Antonio, C.M. & Cooper, S.D. (1990). Mechanisms and consequences of interspecific competition between two stream insects. *Journal of Animal Ecology* 59: 849-866.

Edelstein-Keshet, L. (1988). *Mathematical Models in Biology*. Random House Inc., New York.

Eifert, W.H. & Wesche, T.A. (1982). Evaluation of the Stream Reach Inventory and Channel Stability Index for Instream Habitat Analysis. Water Resources Series No.82. Water Resources Research Institute, University of Wyoming, Laramie, Wyoming.

Elliot, J.M. (1977). Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates. 2nd ed. Freshwater Biological Association Scientific Publication No. 25.

Elton, C.S. (1927). *Animal Ecology*. Sidgwick & Jackson, London.

Elton, C.S. (1933). *The Ecology of Animals*. Reprinted 1966 by Science Paperbacks and Methuen, London.

Elton, C.S. (1958). *The Ecology of Invasion by Animals and Plants*. Methuen, London.

Emmons, L.H. (1980). Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs* 50: 31-54.

Engen, S. (1978). *Stochastic Abundance Models with Emphasis on Biological Communities and Species Diversity*. Chapman & Hall, London.

Fisher, R.A.; Corbet, A.S. & Williams, C.B. (1943). The relation between the number of species and the number of individuals in a random sample from an animal population. *Journal of Animal Ecology* 12: 42-58.

Fisher, S.G.; Gray, L.J.; Grimm, N.B. & Busch, D.E. (1982). Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs* 52: 93-110.

Foged, N. (1979). Diatoms in New Zealand, the North Island. *Bibliotheca Phycologica Band* 47.

Fraleigh, J.B. & Beauregard, R.A. (1989). *Linear Algebra*. 2nd ed. Addison-Wesley Pub. Co., Inc., Reading, Massachusetts.

Frid, C.L.J. & Townsend, C.R. (1989). An appraisal of the patch dynamics concept in stream and marine benthic communities whose members are highly mobile. *Oikos* 56: 137-141.

Frontier, S. (1985). Diversity and structure in aquatic ecosystems. In *Oceanography and Marine Biology - an Annual Review, 23* (ed. M. Barnes), pp. 253-312. Aberdeen University Press, Aberdeen.

Fuller, B.A.G. (1945). *A History of Philosophy*. Henry Holt and Company, New York.

Gage, M. (1959). On the origin of some lakes in Canterbury. *New Zealand Geographer* 15: 69-75.

Gage, M. (1977). Glacial geology. In *Cass: History and Science in the Cass District, Canterbury, New Zealand* (ed. C.J. Burrows), pp. 67-78. Department of Botany Publication, University of Canterbury, Christchurch, New Zealand.

Gardner, M.R. & Ashby, W.R. (1970). Connectance of large, dynamical

(cybernetic) systems: critical values for stability. *Nature* 228: 784.

Gibson, A.S. (1978). Effects of Catchment Use on Some High-Country Lakes in Canterbury. Unpublished M.Sc. Thesis, Joint Centre for Environmental Sciences, University of Canterbury and Lincoln College, Christchurch, New Zealand.

Giller, P.J. (1984). *Community Structure and the Niche.* Chapman and Hall, London.

Giller, P.S. & Gee, J.H.R. (1987). The analysis of community organization: the influence of equilibrium, scale and terminology. In *Organization of Communities Past and Present* (eds. J.H.R. Gee & P.S. Giller), pp. 519-542. 27th Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Gleason, H. (1922). On the relation between species and area. *Ecology* 3: 156-162.

Gleason, H. (1926). The individualistic concept of the plant association. *Bulletin, Torrey Botanical Club* 53: 1-20.

Goh, B.S. (1979). Robust stability concepts for ecosystem models. In *Theoretical Systems in Ecology* (ed. E. Halfon), pp. 467-487. Academic Press, New York.

Golterman, H.L. (1970). Methods for Chemical Analysis of Fresh Waters. 2nd ed. I.B.P. Handbook No. 8. Blackwell Scientific Publications, Oxford.

Goodman, D. (1975). The theory of diversity-stability relationships in ecology. *The Quarterly Review of Biology* 50: 237-266.

Gore, J.A. (1979). Patterns of initial benthic recolonization of a reclaimed coal strip-mined river channel. *Canadian Journal of Zoology* 57: 2429-2439.

Gorman, M. (1979). *Island Ecology. Outline Studies in Ecology.* Chapman and Hall, London.

Graesser, A.K. (1988). Physico-Chemical Conditions and Benthic Community Dynamics in Four South Westland Streams. Unpublished Ph.D. Thesis, University of Canterbury, Christchurch, New Zealand.

Gray, J.S. (1981b). *The Ecology of Marine Sediments.* Cambridge University Press, Cambridge.

Gray, J.S. (1987). Species-abundance patterns. In *Organisation of Communities:*

Past and Present (eds. J.H.R. Gee & P.S. Giller), pp. 53-67. 27th Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Gray, J.S.; Valderhaug, V. & Ugland, K.I. (1985). The stability of a benthic community of soft sediment. In *Proceedings of the 19th European Marine Biology Symposium, Plymouth, 1984* (ed. P.E. Gibbs), pp. 245-253. Cambridge University Press, Cambridge.

Gray, L.J. (1981a). Species composition and life history of aquatic insects in a lowland Sonoran desert stream. *American Midland Naturalist* 106: 229-242.

Greenland, D.E. (1977). Weather and climate at Cass. In *Cass: History and Science in the Cass District, Canterbury, New Zealand* (ed. C.J. Burrows), pp. 93-116. Department of Botany Publication, University of Canterbury, Christchurch, New Zealand.

Gregory, S.V. (1983). Plant-herbivore interactions in stream systems. In *Stream Ecology. Application and Testing of General Ecological Theory* (eds. J.R. Barnes & G.W. Minshall), pp. 157-189. Plenum Press, New York.

Griffiths, G.A. (1979). High sediment yields from major rivers of the western Southern Alps, New Zealand. *Nature* 282: 61-63.

Grime, J.P. (1973). Control of species density in herbaceous vegetation. *Journal of Environmental Management* 1: 151-167.

Grimm, N.B. & Fisher, S.G. (1986). Nitrogen limitation in a Sonoran Desert stream. *Journal of the North American Benthological Society* 5: 2-15.

Grimm, N.B. & Fisher, S.G. (1989). Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8: 293-307.

Grinnell, J. (1917). The niche-relationships of the California Thrasher. *Auk* 34: 427-433.

Grinnell, J. (1924). Geography and evolution. *Ecology* 5: 225-229.

Grinnell, J. (1928). Presence and absence of animals. University of California Chronicle 30: 429-450. (Reprinted in Grinnell, J. (1943). *Joseph Grinnell's Philosophy of Nature*, pp. 187-208. University of California Press, Berkeley and Los Angeles).

Grossman, G.D. (1982). Dynamics and organisation of a rocky intertidal fish

assemblage: the persistence and resilience of taxocene structure. *American Naturalist* 119: 611-637.

Hanski, I. (1978). Some comments on the measurement of niche metrics. *Ecology* 59: 168-174.

Harrison, G.W. (1979). Stability under environmental stress: resistance, resilience, persistence, and variability. *American Naturalist* 113: 659-669.

Hart, D.D. (1983). The importance of competitive interactions within stream populations and communities. In *Stream Ecology. Application and Testing of General Ecological Theory* (eds. J.R. Barnes & G.W. Minshall), pp. 99-136. Plenum Press, New York.

Hart, D.D. (1985). Causes and consequences of territoriality in a grazing stream insect. *Ecology* 66: 404-414.

Hassell, M.P. (1979). *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, Princeton, New Jersey.

Hastings, H.H. & Conrad, M. (1979). Length and evolutionary stability of food chains. *Nature* 282: 838-839.

Hawkins, C.P. & Furnish, J.K. (1987). Are snails important competitors in stream ecosystems? *Oikos* 49: 209-220.

Hawkins, C.P.; Murphy, M.L. & Anderson, N.H. (1982). Effects of canopy, substrate composition and gradient on the structure of macroinvertebrate communities in Cascade Range streams in Oregon. *Ecology* 63: 1840-1856.

Hawkins, C.P. & Sedell, J.R. (1981). Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* 62: 387-397.

Hayward, J.A. (1974). The Waimakariri River. *New Zealands Nature Heritage* 2: 481-488. Hamlyns Limited, Hong Kong.

Hemphill, N. (1988). Competition between two stream dwelling filter-feeders, *Hydropsyche oslari* and *Simulium virgatum*. *Oecologia* 77: 73-80.

Hemphill, N. & Cooper, S.D. (1983). The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. *Oecologia* 58: 378-383.

Hendrix, S.D. (1980). An evolutionary and ecological perspective of the insect

fauna of ferns. *American Naturalist* 115: 171-196.

Hildrew, A.G. & Townsend, C.R. (1987). Organization in freshwater benthic communities. In *Organization of Communities Past and Present* (eds. J.H.R. Gee & P.S. Giller), pp. 347-371. 27th Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Hildrew, A.G.; Townsend, C.R. & Francis, J. (1984). Community structure in some southern English streams: the influence of species interactions. *Freshwater Biology* 14: 297-310.

Hildrew, A.G.; Townsend, C.R. & Hasham, A. (1985). The predatory Chironomidae of an iron-rich stream: feeding ecology and food web structure. *Ecological Entomology* 10: 403-413.

Hill, W.R. & Knight, A.W. (1988). Concurrent grazing effects of two stream insects on periphyton. *Limnology and Oceanography* 33: 15-26.

Hintze, J.L. (1988). *SOLO (User's Guide) Advance Set.* BMDP Statistical Software, Inc. Los Angeles, California.

Holling, C.S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 1-23.

Hughes, R.G. (1985). An hypothesis concerning the influence of competition and stress on the structure of benthic communities. In *Proceedings of the 19th European Marine Biology Symposium, Plymouth, 1984* (ed. P.E. Gibbs), pp. 391-400. Cambridge University Press, Cambridge.

Hughes, R.G. (1986). Theories and models of species abundance. *American Naturalist* 128: 879-899.

Hurlbert, S.H. (1971). The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52: 577-586.

Hurlbert, S.H. (1978). The measurement of niche overlap and some relatives. *Ecology* 59: 67-77.

Huston, M. (1979). A general hypothesis of species diversity. *American Naturalist* 113: 81-101.

Hutchinson, G.E. (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93: 145-159.

Hutchinson, G.E. (1978). *An Introduction to Population Ecology.* Yale University Press, New Haven.

Hynes, H.B.N. (1970). *The Ecology of Running Waters*. University of Toronto Press, Toronto.

Hynes, H.B.N. (1975). The stream and its valley. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 19: 1-15.

Jeffries, M.J. & Lawton, J.H. (1985). Predator-prey ratios in communities of freshwater invertebrates: the role of enemy free space. *Freshwater Biology* 15: 105-112.

Jowett, I.G. & Duncan, M.J. (1990). Flow variability in New Zealand rivers and its relationship to in-stream habitat and biota. *New Zealand Journal of Marine and Freshwater Research* 24: 305-317.

Kempton, R.A. & Taylor, L.R. (1974). Log-series and log-normal parameters as diversity discriminants for the Lepidoptera. *Journal of Animal Ecology* 43: 381-399.

Kempton, R.A. & Taylor, L.R. (1976). Models and statistics for species diversity. *Nature* 262: 818-820.

Kikkawa, J. (1986). Complexity, diversity and stability. In *Community Ecology: Pattern and Process* (eds. J. Kikkawa & D.J. Anderson), pp. 41-62. Blackwell Scientific Publications, Oxford.

King, C.E. (1964). Relative abundance of species and MacArthur's model. *Ecology* 45: 716-727.

Kishimoto, K. (1988). A stable spatially non-constant equilibrium of Lotka-Voltera two-patch system with May-Leonard dynamics. In *Biomathematics and Related Computational Problems* (ed. L.M. Ricciardi), pp. 331-335. Reidel, Amsterdam.

Kishimoto, K. (1990). Coexistence of any number of species in the Lotka-Volterra competitive system over two patches. *Theoretical Population Biology* 38: 149-158.

Kitching, R.L. (1983). Community structure in water-filled treeholes in Europe and Australia - comparisons and speculations. In *Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities* (eds. J.H. Frank & L.P. Lounibos), pp. 205-222. Plexus, Medford, New Jersey.

Kitching, R.L. & Pimm, S.L. (1985). The length of food chains: Phytotelmata in Australia and elsewhere. *Proceedings of the Ecological Society of Australia* 14: 123-140.

Krebs, C. J. (1985). *Ecology: The Experimental Analysis of Distribution and Abundance*. 3rd ed. Harper & Row Publishers, New York.

Krebs, J.R. (1978). Optimal foraging: decision rules for predators. In *Behavioural Ecology: An Evolutionary Approach* (eds. J.R. Krebs & N.B. Davies), pp. 23-63. Sinauer Associated Ltd., Sunderland, Massachusetts.

Krumholz, L.A. & Neff, S.E. (1970). The freshwater stream, a complex ecosystem. *Water Resources Bulletin* 6: 163-174.

Ladle, M.; Cooling, D.A.; Welton, J.S. & Bass, J.A.B. (1985). Studies on Chironomidae in experimental recirculating stream systems. II. The growth development and production of a spring generation of *Orthocladius* (*Euorthocladius*) *calvus* Pinder. *Freshwater Biology* 15: 243-255.

Lake, P.S. (1986). Stream communities and the management of streams. In *Stream Protection: The Management of Rivers for Instream Uses* (ed. I.C. Campbell), pp. 3-21. Water Study Centre, Chisholm Institute of Technology, East Caulfield, Australia.

Lake, P.S. (1990). Disturbing hard and soft bottom communities: a comparison of marine and freshwater environments. *Australian Journal of Ecology* 15: 477-488.

Lake, P.S. & Barmuta, L.A. (1986). Stream benthic communities: Persistent presumptions and current speculations. In *Limnology in Australia* (eds. P. De Deckker & W.D. Williams), pp. 263-276. CSIRO/Dr W. Junk Publishers, Melbourne.

Lake, P.S.; Barmuta, L.A.; Boulton, A.J.; Campbell, I.C. & St Clair, R.M. (1985). Australian streams and Northern Hemisphere stream ecology: comparisons and problems. *Proceedings of the Ecological Society of Australia* 14: 61-82.

Lake, P.S.; Doeg, T.J. & Marchant, R. (1989). Effects of multiple disturbance on macroinvertebrate communities in the Acheron River, Victoria. *Australian Journal of Ecology* 14: 507-514.

Lake, P.S.; Morton, D.W. & Milne, B.J. (1988). Interspecific associations in the faunal assemblages of stones of an upland Australian stream. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 1384-1387.

Lamberti, G.A. & Resh, V.H. (1983). Stream periphyton and insect herbivores:

an experimental study of grazing by a caddisfly population. *Ecology* 64: 1124-1135.

Lambshead, J. & Platt, H.M. (1985). Structural patterns of marine benthic assemblages and their relationships with empirical statistical models. In *Proceedings of the 19th European Marine Biology Symposium, Plymouth, 1984* (ed. P.E. Gibbs), pp. 371-380. Cambridge University Press, Cambridge.

Lane, E.W. (1955). Design of stable channels. *Transactions of the American Society of Civil Engineers* 120: 1234-1260.

Lawlor, L.R. (1980a). Structure and stability in natural and randomly constructed competitive communities. *American Naturalist* 116: 394-408.

Lawlor, L.R. (1980b). Overlap, similarity, and competition coefficients. *Ecology* 61: 245-251.

Lawton, J.H. (1989). Food Webs. In *Ecological Concepts* (ed. J.M. Cherret), pp. 43-78. 75th Anniversary Symposium British Ecological Society. Blackwell Scientific Publications, Oxford.

Lawton, J.H. & Warren, P.H. (1988). Static and dynamic explanations for patterns in food webs. *Trends in Ecology and Evolution* 3: 242-245.

Legendre, L. & Legendre, P. (1983). *Numerical Ecology*. Elsevier, New York.

Levins, R. (1968). *Evolution in Changing Environments: Some Theoretical Explanations*. Princeton University Press, Princeton, New Jersey.

Levins, R.; Pressick, M.L. & Heatwole, H. (1973). Coexistence patterns in insular ants. *American Scientist* 61: 463-472.

Levitan, C. (1987). Formal stability analysis of a planktonic freshwater community. In *Predation Direct and Indirect Impacts on Aquatic Communities* (eds. W.C. Kerfoot & A. Sih), pp. 71-100. University Press of New England, Hanover.

Lewontin, R.C. (1969). The meaning of stability. *Brookhaven Symposia in Biology* 22: 13-34.

Liapunov, A.M. (1907). Problème général de la stabilité du mouvement'. *Annals of Mathematics. Studies* No. 7, Princeton University Press, Princeton. (French translation of 1892 paper in Russian).

Lindstrom, E.A. & Traaen, T.S. (1984). Influence of current velocity on

periphyton distribution and succession in a Norwegian soft water stream. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 22: 1965-1972.

Lubchenco, J. (1978). Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112: 23-39.

Lubchenco, J. & Gaines, S.D. (1981). A unified approach to marine plant herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* 12: 405-437.

Ludwig, J.A. & Reynolds, J.F. (1988). *Statistical Ecology. A Primer on Methods and Computing*. John Wiley & Sons, New York.

MacArthur, J.W. (1975). Environmental fluctuations and species diversity. In *Ecology and Evolution of Communities* (eds. M.L. Cody & J.M. Diamond), pp. 74-80. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

MacArthur, R.H. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533-536.

MacArthur, R.H. (1957). On the relative abundance of bird species. *Proceedings of the National Academy of Science, USA* 43: 293-295.

MacArthur, R.H. (1960). On the relative abundance of species. *American Naturalist* 94: 25-36.

MacArthur, R.H. (1968). The theory of the niche. In *Population Biology and Evolution* (ed. R.C. Lewontin), pp. 159-176. Syracuse University Press, Syracuse, New York.

MacArthur, R.H. (1972). *Geographical Ecology. Patterns in the Distribution of Species*. Harper & Row Publishers, New York.

MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* 101: 377-385.

McAuliffe, J.R. (1983). Competition, colonization patterns, and disturbance in stream benthic communities. In *Stream Ecology. Application and Testing of General Ecological Theory* (eds. J.R. Barnes & G.W. Minshall), pp. 137-156. Plenum Press, New York.

McAuliffe, J.R. (1984a). Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65: 894-908.

McAuliffe, J.R. (1984b). Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. *Oikos* 42: 327-333.

M'Closkey, R.T. (1978). Niche separation and assembly in four species of Sonoran desert rodents. *American Naturalist* 112: 683-694.

McConnell, W.J. & Sigler, W.F. (1959). Chlorophyll and productivity in a mountain river. *Limnology and Oceanography* 4: 335-351.

McCune, B. (1987). Multivariate analysis on the PC-ORD system. HRI Report No. 75. Butler University, Indianapolis, Indiana.

McElravy, E.P.; Lamberti, G.A. & Resh, V.H. (1989). Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the North American Benthological Society* 8: 51-63.

McFarlane, A.G. (1951). Caddisfly larvae (Trichoptera) of the family Rhyacophilidae. *Records of the Canterbury Museum 5*: 267-289.

McGuinnness, K.A. (1987). Disturbance and organisms on boulders. II. Causes of patterns of diversity and abundance. *Oecologia* 71: 420-430.

McIntire (1968). Structural characteristics of benthic algal communities in laboratory streams. *Ecology* 49: 520-537.

McIntosh, R.P. (1987). *The Background of Ecology. Concept and Theory.* Cambridge University Press, Cambridge.

McNaughton, S.J. (1978). Stability and diversity of ecological communities. *Nature* 274: 251-253.

McNaughton, S.J. (1988). Diversity and stability. *Nature* 333: 204-205.

Macan, T.T. (1963). *Freshwater Ecology.* J. Wiley & Sons, New York.

Maciolek, J.A. (1962). Limnological organic analyses by quantitative dichromate oxidation. United States Department of the Interior Research Report No. 60.

Mackay, R.J., & Kalff, J. (1969). Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. *Ecology* 50: 101-109.

Mackereth, F.H.J. (1963). Some Methods of Water Analysis for Limnologists. Freshwater Biological Association Publication No. 21.

Magurran, A.G. (1988). *Ecological Diversity and its Measurement.* Croom Helm Limited, London.

Malmqvist, B. & Otto, C. (1987). The influence of substrate stability on the composition of stream benthos: an experimental study. *Oikos* 48: 33-38.

Malmqvist, B. & Sjostrom, P. (1984). The microdistribution of some lotic insect predators in relation to their prey and to abiotic factors. *Freshwater Biology* 14: 649-656.

Mandelbrot, B.B. (1977). *Fractals. Form, Chance and Dimension.* W.H. Freeman, San Francisco.

Marchant, R.; Metzeling, L.; Graesser, A. & Suter, P. (1985). The organization of macroinvertebrate communities in the major tributaries of the LaTrobe River, Victoria, Australia. *Freshwater Biology* 15: 315-331.

Matthews, W.J. (1986). Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. *Copeia* 1986: 388-397.

May, R.M. (1972). Will a large complex system be stable? *Nature* 238: 413-414.

May, R.M. (1973). *Stability and Complexity in Model Ecosystems.* Princeton University Press, Princeton, New Jersey.

May, R.M. (1974). On the theory of niche overlap. *Theoretical Population Biology* 5: 297-332.

May, R.M. (1975). Patterns of species abundance and diversity. In *Ecology and Evolution of Communities* (eds. M.L. Cody & J.M. Diamond), pp. 81-120. Belknap Press, Harvard.

May, R.M. (1979). The structure and dynamics of ecological systems. In *Population Dynamics* (eds. R.M. Anderson; B.D. Turner & L.R. Taylor), pp. 385-407. 20th Symposium of the British Ecological Society. Blackwell, Oxford

May, R.M. (1981). Patterns in multi-species communities. In *Theoretical Ecology: Principles and Applications* (ed. R.M. May), pp. 197-227. Blackwell, Oxford.

May, R.M. (1986). The search for patterns in the balance of nature: advances and retreats. *Ecology* 67: 1115-1126.

May, R.M. & MacArthur, R.H. (1972). Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences, USA* 69: 1109-1113.

Meffe, G.K. & Minckley, W.L. (1986). Persistence and stability of fish and

invertebrate assemblages in a repeatedly disturbed Sonoran desert stream. *American Midland Naturalist* 117: 177-191.

Menge, B.A. & Sutherland, J.P. (1976). Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *American Naturalist* 110: 351-369.

Menge, B.A. & Sutherland, J.P. (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130: 730-757.

Merritt, R.W. & Cummins, K.W. (1984). *An Introduction to the Aquatic Insects of North America.* Kendall/Hunt Publishing Company, Dubuque, Iowa.

Miller, T.E. (1982). Community diversity and interactions between the size and frequency of disturbance. *American Naturalist* 120: 533-536.

Minckley, W.L. (1963). The ecology of a spring stream, Doe Run, Meade County, Kentucky. *Wildlife Monographs* 11: 1-124.

Minshall, G.W. (1978). Autotrophy in stream ecosystems. *Bioscience* 28: 767-771.

Minshall, G.W. (1988). Stream ecosystem theory: a global perspective. *Journal of the North American Benthological Society* 7: 263-288.

Minshall, G.W. & Petersen, R.C. (1985). Towards a theory of macroinvertebrate community structure in stream ecosystems. *Archive für Hydrobiologie* 104: 49-76.

Minshall, G.W.; Peterson Jr., R.C. & Nimz, C.F. (1985). Species richness in streams of different size from the same drainage basin. *American Naturalist* 125: 16-38.

Moar, N.T. & Lintott, W.H. (1977). Post-glacial history of vegetation at Cass. In *Cass: History and Science in the Cass District, Canterbury, New Zealand* (ed. C.J. Burrows), pp. 147-156. Department of Botany Publication, University of Canterbury, Christchurch, New Zealand.

Moler, C.; Little, J. & Bangert, S. (1987). *PC-MATLAB for MS-DOS Personal Computers: User's Guide.* The Math Works, Inc., Sherborn, Massachusetts.

Molloy, B.P.J. (1969). Recent history of the vegetation. In *The Natural History of Canterbury* (ed. G.A. Knox), pp. 340-360. A.H. & A.W. Reed Ltd., Wellington.

Moran, V.C. & Southwood, T.R.E. (1982). The guild composition of arthropod communities in trees. *Journal of Animal Ecology* 51: 289-306.

Moss, B. (1967a). A spectrophotometric method for the estimation of percentage degradation of chlorophylls to pheo-pigments in extracts of algae. *Limnology and Oceanography* 12: 335-340.

Moss, B. (1967b). A note on the estimation of chlorophyll a in freshwater algal communities. *Limnology and Oceanography* 12: 307-342.

Moss, D.; Furse, M.T.; Wright, J.F. & Armitage, P.D. (1987). The prediction of the macro-invertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. *Freshwater Biology* 17: 41-52.

Motomura, I. (1932). A statistical treatment of associations (in Japanese). *Zoological Magazine, Tokyo* 44: 379-383.

New Zealand Meterological Service. (1983). Summaries of Climatological Observations to 1980. New Zealand Meterological Service Miscellaneous Publication No. 177.

Newbury, R.W. (1984). Hydrologic determinants of aquatic insect habitats. In *The Ecology of Aquatic Insects* (eds. V.H. Resh & D.M. Rosenberg), pp. 323-357. Praeger Publishers, New York.

Newell, R.I.E. (1982). An evaluation of the wet oxidation technique for use in determining the energy content of seston samples. *Canadian Journal of Fisheries and Aquatic Sciences* 39: 1383-1388.

Newman, J.E. & Cohen, J.E. (1986). A stochastic theory of community food webs. IV. Theory of food chain lengths in large webs. *Proceedings of the Royal Society of London B* 228: 355-377.

Noy-Meir, I. & Whittaker, R.H. (1977). Continuous multivariate methods in community analysis: Some problems and developments. *Vegetatio* 33: 79-98.

Oksanen, L.; Fretwell, S.D.; Arruda, J. & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118: 240-262.

Ordish, R.G. (1984). Hydraenidae (Insecta: Coleoptera). Fauna of New Zealand No. 6. Science Information Publishing Centre, DSIR, Wellington.

Paine, R.T. (1966). Food web complexity and species diversity. *American Naturalist* 100: 65-75.

Patrick, R. (1973). Use of algae, especially diatoms, in the assessment of water quality. *American Society for Testing and Materials, Special Technical Publication* 528: 7-95.

Peckarsky, B.L. (1983). Biotic interactions or abiotic limitations? A model of lotic community structure. In *Dynamics of Lotic Ecosystems* (eds. T.D. Fontaine III & S.M. Bartell), pp. 303-323. Ann Arbor Scientific Publications, Michigan, U.S.A.

Peckarsky, B.L. (1984). Predator-prey interactions among aquatic insects. In *The Ecology of Aquatic Insects* (eds. V.H. Resh & D.M. Rosenberg), pp. 196-254. Praeger Publishers, New York.

Peckarsky, B.L. (1986). Colonization of natural substrates by stream benthos. *Canadian Journal of Fisheries and Aquatic Science* 43: 700-709.

Peckarsky, B.L. (1988). Why predaceous stoneflies do not aggregate with their prey. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 23: 2135-2140.

Peckarsky, B.L.; Horn, S.C. & Statzner, B. (1990). Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. *Freshwater Biology* 24: 181-191.

Peterson, B.J.; Hobbie, J.E.; Hershey, A.E.; Lock, M.A.; Ford, T.E.; Vestal, J.R.; McKinley, J.L.; Hullar, M.A.J.; Miller, M.C.; Ventullo, R.M. & Volk, G.S. (1985). Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. *Science* 229: 1383-1386.

Petraitis, P.S.; Latham, R.E. & Niessenbaum, R.A. (1989). The maintenance of species diversity by disturbance. *The Quarterly Review of Biology* 64: 393-418.

Pfankuch, D. J. (1975). Stream reach inventory and channel stability evaluation. U.S.D.A. Forest Service, Region 1. Missoula, Montana, U.S.A.

Pianka, E.R. (1967). Lizard species diversity. *Ecology* 48: 333-351.

Pianka, E.R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53-74.

Pianka, E.R. (1974). Niche overlap and diffusion competition. *Proceedings of the National Academy of Sciences, USA* 71: 2141-2145.

Pianka, E.R. (1975). Niche relations of desert lizards. In *Ecology and Evolution of Communities* (eds. M. Cody & J.M. Diamond), pp. 292-314. Belknap Press

of Harvard University Press, Cambridge, Massachusetts.

Pianka, E.R. (1981). Competition and niche theory. In *Theoretical Ecology: Principles and Applications* 2nd ed. (ed. R.M. May), pp. 167-196. Blackwell Scientific Publications, Oxford.

Pianka, E.R. (1983). *Evolutionary Ecology*. 3rd ed. Harper & Row Publishers, New York.

Pickett, S.T.A. & White, P.S. (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.

Pielou, E.C. (1972). Niche width and overlap: a method for measuring them. *Ecology* 53: 687-692.

Pielou, E.C. (1975). *Ecological Diversity*. Wiley Interscience, New York.

Pielou, E.C. (1984). *The Interpretation of Ecological Data*. Wiley, New York.

Pimm, S.L. (1979a). The structure of food webs. *Theoretical Population Biology* 16: 144-158.

Pimm, S.L. (1979b). Complexity and stability: another look at MacArthur's original hypothesis. *Oikos* 33: 351-357.

Pimm, S.L. (1982). *Food Webs*. Chapman & Hall, London.

Pimm, S.L. (1985). Estimating competition coefficients from census data. *Oecologia* 67: 588-590.

Pimm, S.L. & Kitching, R.L. (1987). The determinants of food chain length. *Oikos* 50: 302-307.

Pimm, S.L. & Lawton, J.H. (1977). Number of trophic levels in ecological communities. *Nature* 268: 329-331.

Pimm, S.L. & Lawton, J.H. (1978). On feeding on more than one trophic level. *Nature* 275: 542-544.

Pimm, S.L. & Lawton, J.H. (1983). The causes of food web structure: dynamics, energy flow and natural history. In *Current Trends in Food Web Theory. Report on a Food Web Workshop* (eds. D.L. DeAngelis; W.M. Post & G. Sugihara), pp. 45-49. Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Pinder, L.C.V. (1985). Studies on Chironomidae in experimental recirculating streams. I. *Orthocladius* (*Euorthocladius*) *calvus* sp. nov. *Freshwater Biology* 15: 235-241.

Poole, R.W. (1974). *An Introduction to Quantitative Ecology*. McGraw-Hill Kogakusha, Tokyo.

Porter, J.H. & Dueser, R.D. (1982). Niche overlap and competition in an insular small mammal fauna: a test of the niche overlap hypothesis. *Oikos* 39: 228-236.

Power, M.E. & Stewart, A.J. (1987). Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. *American Midland Naturalist* 117: 333-345.

Power, M.E.; Stout, R.J.; Cushing, C.E.; Harper, P.P.; Hauer, F.R.; Matthews, W.J.; Moyle, P.B.; Statzner, B. & Wais de Badgen, I.R. (1988). Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7: 456-479.

Preston, F.W. (1948). The commonness and rarity of species. *Ecology* 29: 254-283.

Pridmore, R.D. (1985). Use of the Cochran Q-test in analysing species presence-absence data in freshwater biological studies. In *Biological Monitoring in Freshwaters: Proceedings of a Seminar* (eds. R.D. Pridmore & A.B. Cooper), pp. 27-38. Water & Soil Miscellaneous Publication 82.

Pridmore, R.D. & Hewitt, J. (1982). A Guide to the Common Freshwater Algae in New Zealand. Water & Soil Miscellaneous Publication No. 39. Water and Soil Conservation Organisation, Wellington.

Pringle, C.M.; Naiman, R.J.; Bretschko, G.; Karr, J.R.; Oswood, M.W.; Webster, J.R.; Welcomme, R.L. & Winterbourn, M.J. (1988). Patch dynamics in lotic systems: the stream as a mosaic. *Journal of the North American Benthological Society* 7: 503-524.

Quinn, J.M. & Hickey, C.W. (1990a). Characterisation and classification of benthic invertebrate communities in 88 New Zealand rivers in relation to environmental factors. *New Zealand Journal of Marine and Freshwater Research* 24: 387-409.

Quinn, J.M. & Hickey, C.W. (1990b). Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 24: 411-427.

Rader, R.B. & Ward, J.V. (1989). The influence of environmental predictability/

disturbance characteristics on the structure of a guild of mountain stream insects. *Oikos* 54: 107-116.

Reice, S.R. (1981). Interspecific associations in a woodland stream. *Canadian Journal of Fisheries and Aquatic Science* 38: 1271-1280.

Reice, S.R. (1983). Predation and substratum: factors in lotic community structure. In *Dynamics of Lotic Ecosystems* (eds. T.D. Fontaine III & S.M. Bartell), pp. 325-345. Ann Arbor Science, Ann Arbor, U.S.A.

Reice, S.R. (1984). The impact of disturbance frequency on the structure of a lotic riffle community. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 22: 1906-1910.

Reice, S.R. (1985). Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia* 67: 90-97.

Rejmanek, M. & Stary, P. (1979). Connectance in real biotic communities and critical values for stability of model ecosystems. *Nature* 280: 311-313.

Relph, D.H. (1957). The vegetation cover of the Castle Hill Basin. *New Zealand Geographer* 13: 41-55.

Relph, D.H. (1958). A century of human influence on high country vegetation. *New Zealand Geographer* 14: 131-146.

Resh, V.H.; Brown, A.V.; Covich, A.P.; Gurtz, M.E.; Li, H.W.; Minshall, G.W.; Reice, S.R.; Sheldon, A.L.; Wallace, J.B. & Wissmar, R.C. (1988). The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7: 433-455.

Robinson, C. T. & Minshall, G. W. (1986). Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *Journal of the North American Benthological Society* 5: 237-248.

Rosenzwerg, M.L.; Abramsky, Z.; Kotler, B. & Mitchell, W. (1985). Can interaction coefficients be determined from census data? *Oecologia* 66: 194-198.

Roughgarden, J. (1989). The structure and assembly of communities. In *Perspectives in Ecological Theory* (eds. J. Roughgarden; R.M. May & S.A. Levin), pp. 203-226. Princeton University Press, Princeton, New Jersey.

Rounick, J.S. & Gregory, S.V. (1981). Temporal changes in periphyton standing crop during an unusually dry winter in streams of the Western Cascades, Oregon. *Hydrobiologia* 83: 197-205.

Rounick, J.S. & Winterbourn, M.J. (1982). Benthic faunas of forested streams and suggestions for their management. *New Zealand Journal of Ecology* 5: 140-150.

Rounick, J.S. & Winterbourn, M.J. (1983a). Leaf processing in two contrasting beech forest streams: effects of physical and biotic factors in litter breakdown. *Archive für Hydrobiologie* 96: 448-474.

Rounick, J.S. & Winterbourn, M.J. (1983b). The formation, structure and utilisation of stone surface organic layers in two New Zealand streams. *Freshwater Biology* 13: 57-72.

Ryder, G.I. (1989). Experimental Studies on the Effects of Fine Sediments on Lotic Invertebrates. Unpublished Ph.D. Thesis, University of Otago, Dunedin, New Zealand.

SAS (1985). *SAS User's Guide: Statistics, Version 5 Edition*. SAS Institute Inc., Cary, North Carolina.

Sagar, P.M. (1986). The effects of floods on the invertebrate fauna on a large unstable braided river. *New Zealand Journal of Marine and Freshwater Research* 20: 37-46.

Sale, P.F. (1977). Maintenance of high diversity in coral reef fish communities. *American Naturalist* 111: 337-359.

Sale, P.F. (1980a). The ecology of fishes in coral reefs. *Oceanography and Marine Biology: An Annual Review* 18: 367-421.

Sale, P.F. (1980b). Assemblages of fish on patch reefs - predictable or unpredictable? *Environmental Biology of Fishes* 5: 243-249.

Schluter, D. (1984). A variance test for detecting species associations, with some example applications. *Ecology* 65: 998-1005.

Schoener, T.W. (1970). Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408-418.

Schoener, T.W. (1974). Competition and the form of habitat shift. *Theoretical Population Biology* 6: 265-307.

Schoener, T.W. (1986a). Kinds of ecological communities - ecology becomes pluralistic. In *Community Ecology* (eds. J. Diamond & T.J. Case), pp. 467-479. Harper & Row Publishers, New York.

Schoener, T.W. (1986b). Resource partitioning. In *Community Ecology: Pattern and Process* (eds. J. Kikkawa & D. Anderson), pp. 91-126. Blackwell Scientific Publications, Oxford.

Schoener, T.W. (1988). Ecological interactions. In *Analytical Biogeography: an Integrated Approach to the Study of Animal and Plant Distribution* (eds. A.A. Myers & P.S. Giller), pp. 255-297. Chapman and Hall, London.

Schoener, T.W. (1989). The ecological niche. In *Ecological Concepts* (ed. J.M. Cherret), pp. 79-113. 75th Anniversary Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Scrimgeour, G.J.; Culp, J.M.; Bothwell, M.L.; Wrona, F.J. & McKee, M.H. (1991). Mechanisms of algal patch depression: importance of consumptive and non-consumptive losses in mayfly-diatom systems. *Oecologia* 85: 343-348.

Scrimgeour, G.J.; Davidson, R.J. & Davidson, J.M. (1988). Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 22: 337-344.

Scrimgeour, G.J. & Winterbourn, M.J. (1989). Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia* 171: 33-44.

Seifert, R.P. & Seifert, F.H. (1976). A community matrix analysis of *Helicona* insect communities. *American Naturalist* 110: 461-483.

Shaw, K.M.; Lambshead, P.J.D. & Platt, H.M. (1983). Detection of pollution induced disturbance in marine benthic assemblages with special reference to nematodes. *Marine Ecology. Progress Series* 11: 195-202.

Sheldon, A.L. (1977). Colonization curves: application to stream insects on semi-natural substrates. *Oikos* 28: 256-261.

Sheldon, A.L. (1984). Colonization dynamics of aquatic insects. In *The Ecology of Aquatic Insects* (eds. V.H. Resh & D.M. Rosenberg), pp. 401-429. Praeger Publishers, New York.

Shepard, R.B. (1984). The logseries distribution and Mountford's similarity index as a basis for the study of stream benthic community structure. *Freshwater Biology* 14: 53-71.

Shirazi, M.A. & Seim, W.K. (1979). A stream systems evaluation - an emphasis on spawning habitat for salmonids. Corvallis Environmental Research Laboratory, Corvallis, Oregon.

Siegel, S. (1956). *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill Book Company, Inc., New York.

Siegfried, C.A. & Knight, A.W. (1977). The effects of a washout in a Sierra foothill stream. *American Midland Naturalist* 98: 200-206.

Simpson, E.H. (1949). Measurement of diversity. *Nature* 163: 688.

Slobodkin, L.B. (1961). *Growth and Regulation of Animal Populations*. Holt, Rinehart & Winston, New York.

Smith, J.N.M.; Grant, P.R.; Grant, B.R.; Abbott, I.J. & Abbott, L.K. (1978). Seasonal variation in feeding habitats of Darwin's ground finches. *Ecology* 59: 1137-1150.

Sokal, R.R. & Rohlf, F.J. (1981). *Biometry*. 2nd ed. W.H. Freeman & Company, San Francisco.

Sousa, W.P. (1979). Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. *Ecology* 60: 1225-1239.

Southwood, T.R.E. (1978). *Ecological Methods with Particular Reference to the Study of Insect Populations*. 2nd ed. Chapman and Hall, London.

Stanford, J.A. & Ward, J.V. (1983). Insect species diversity as a function of environmental variability and disturbance in stream ecosystems. In *Stream Ecology: Application and Testing of General Ecological Theory* (eds. J.R. Barnes & G.W. Minshall), pp. 265-278. Plenum Press, New York.

Stenseth, N.C. (1979). Where have all the species gone? On the nature of extinction and the Red Queen hypothesis. *Oikos* 33: 196-227.

Stout, V.M. (1977). Biology of the fauna of lakes and tarns. In *Cass: History and Science in the Cass District, Canterbury, New Zealand* (ed. C.J. Burrows), pp. 291-309. Department of Botany Publication, University of Canterbury, Christchurch, New Zealand.

Strong, D.R.; Simberloff, D.; Abele, L.G. & Thistle, A.B. (eds.) (1984). *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press, Princeton, New Jersey, U.S.A.

Sugihara, G. (1980). Minimal community structure: an explanation of species abundance patterns. *American Naturalist* 116: 770-787.

Sweeney, B.W. (1978). Bioenergetic and developmental response of a mayfly to thermal variation. *Limnology and Oceanography* 23: 461-477.

Taylor, L.R. (1978). Bates, Williams, Hutchinson - a variety of diversities. In *Diversity of Insect Faunas: 9th Symposium of the Royal Entomological Society* (eds. L.A. Mound & N. Warloff), pp. 1-18. Blackwell Scientific Publications, Oxford.

Tett, P.; Gallegos, C.; Kelly, M.G.; Hornberger, G.M. & Cosby B.J. (1978). Relationships among substrate, flow and benthic microalgal pigment density in the Mechums River, Virginia. *Limnology and Oceanography* 23: 785-797.

Thiery, R.G. (1982). Environmental instability and community diversity. *Biological Reviews* 57: 671-710.

Thoreau, H.D. (1860). The succession of forest trees. In *Excursions (1863)*, Houghton and Mifflin, Boston.

Tokeshi, M. (1986). Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. *Journal of Animal Ecology* 55: 491-506.

Tokeshi, M. (1990). Niche apportionment or random assortment: species abundance patterns revisited. *Journal of Animal Ecology* 59: 1129-1146.

Tokeshi, M. & Townsend, C.R. (1987). Random patch formation and weak competition: coexistence in an epiphytic chironomid community. *Journal of Animal Ecology* 56: 833-845.

Townsend, C.R. (1989). The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8: 36-50.

Townsend, C.R. & Hildrew, A.G. (1984). Longitudinal pattern in detritivore communities of acid streams: a consideration of alternative hypotheses. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 22: 1953-1958.

Townsend, C.R.; Hildrew, A.G. & Francis, J. (1983). Community structure in some southern English streams: the influence of physicochemical factors. *Freshwater Biology* 13: 521-544.

Townsend, C.R.; Hildrew, A.G. & Schofield, K. (1987). Persistence of stream

invertebrate communities in relation to environmental variability. *Journal of Animal Ecology* 56: 597-613.

Triska, F.J.; Kennedy, V.C.; Avanzino, R.J. & Reilly, B.N. (1983). Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. In *The Dynamics of Lotic Systems* (ed. T.D. Fontaine III & S.M. Bartell), pp. 129-159. Ann Arbor Press, Ann Arbor, Michigan, U.S.A.

Trotter, E.H. (1990). Woody debris, forest-stream succession, and catchment geomorphology. *Journal of the North American Benthological Society* 9: 141-156.

Turelli, M. (1981). Niche overlap and invasion of competitors in random environments. I. Models without demographic stochasticity. *Theoretical Population Biology* 20: 1-56.

Ugland, K.I. & Gray, J.S. (1982). Lognormal distributions and the concept of community equilibrium. *Oikos* 39: 171-178.

Vannote, R.L.; Minshall, G.W.; Cummins, K.W.; Sedell, J.R. & Cushing, C.E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

Vannote, R.L. & Sweeney, B.W. (1980). Geographic analysis of thermal equilibria, a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. *American Naturalist* 115: 667-695.

Walde, S.J. (1986). Effect of an abiotic disturbance on a lotic predator-prey interaction. *Oecologia* 690: 243-247.

Walde, S.J. & Davies, R.W. (1984). The effect of intraspecific interference on *Kogotus nonus* (Plecoptera) foraging behaviour. *Canadian Journal of Zoology* 62: 2221-2226.

Walker, D. (1989). Diversity and Stability. In *Ecological Concepts* (ed. J.M. Cherret), pp. 115-145. 75th Anniversary Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

Ward, J.V. & Stanford, J.A. (1983). The intermediate disturbance hypothesis: an explanation for biotic diversity in lotic ecosystems. In *Dynamics of Lotic Ecosystems* (eds. T.D. Fontaine III & S.M. Bartell), pp. 347-35. Ann Arbor Science, Ann Arbor, U.S.A.

Warren, P.H. (1989). Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 55: 299-311.

Warren, P.H. & Lawton, J.H. (1987). Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? *Oecologia* 74: 231-235.

Washington, H.G. (1984). Diversity, biotic and similarity indices: a review with special relevance to aquatic ecosystems. *Water Research* 18: 653-694.

Weber, C.I. (1971). A guide to the common diatoms at water pollution surveillance system stations. U.S. Environmental Protection Agency Report, National Environmental Research Center, Ohio.

Webster, J.; Waide, J.B. & Patten, B.C. (1975). Nutrient cycling and the stability of ecosystems. In *Mineral Cycling in Southeastern Ecosystems* (ed. F.G. Howell), pp. 1-27. Atomic Energy Commission Symposium Series Conference 74-0513.

Webster, J.R.; Benfield, E.F.; Golladay, S.W.; Hill, B.H.; Hornick, L.E.; Kazmierczak Jr., R.F. & Pery, W.B. (1987). Experimental studies of physical factors affecting seston transport in streams. *Limnology and Oceanography* 32: 848-863.

Webster, J.R.; Golladay, S.W.; Benfield, E.F.; D'Angelo, D.J. & Peters, G.T. (1990). Effects of forest disturbance on particulate organic matter budgets of small streams. *Journal of the North American Benthological Society* 9: 120-140.

Wetzel, R.G. & Westlake, D.F. (1974). Sampling techniques and methods for estimating quantity and quality of biomass: periphyton. In *A Manual on Methods for Measuring Primary Production in Aquatic Environments* (ed. R.A. Vollenweider), pp. 33-40. IBP handbook No. 12. Blackwell Scientific Publications, Oxford.

White, P.S. & Pickett, S.T.A. (1985). Natural disturbance and patch dynamics: an introduction. In *The Ecology of Natural Disturbance and Patch Dynamics* (eds. S.T.A. Pickett & P.S. White), pp. 3-13. Academic Press, Orlando.

Whittaker, R.H. (1975). *Communities and Ecosystems*. 2nd ed. Macmillan Publishing Co., Inc., New York.

Whittaker, R.H. (1977). Evolution of species diversity in land communities. In *Evolutionary Biology, 10* (eds. M.K. Hecht; W.C. Steere & B. Wallace), pp. 1-67. Plenum Press, New York.

Williams, C.B. (1964). *Patterns in the Balance of Nature.* Academic Press, London.

Williamson, M.H. (1978). The ordination of incidence data. *Journal of Ecology* 66: 911-920.

Winemiller, K.O. (1989). Must connectance decrease with species richness? *American Naturalist* 134: 960-968.

Winemiller, K.O. (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60: 331-367.

Winterbourn, M.J. (1976). Fluxes of litter falling into a small beech forest stream. *New Zealand Journal of Marine and Freshwater Research* 10: 399-416.

Winterbourn, M.J. (1986). Forestry practices and stream communities with particular reference to New Zealand. In *Stream Protection: The Management of Rivers for Instream Uses* (ed. I.C. Campbell), pp. 57-73. Water Studies Centre, Chisholm Institute of Technology, Australia.

Winterbourn, M.J. (1987). Invertebrate communities. In *Inland Waters of New Zealand* (ed. A.B. Viner), pp. 167-190. DSIR Bulletin 241. DSIR Science Information Publishing Centre, Wellington.

Winterbourn, M.J. (1990). Interactions among nutrients, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biology* 23: 463-474.

Winterbourn, M.J. & Collier, K.J. (1987). Distribution of benthic invertebrates in acid, brown water streams in the South Island of New Zealand. *Hydrobiologia* 153: 277-286.

Winterbourn, M.J.; Cowie, B. & Rounick, J.S. (1984). Food resources and ingestion patterns of insects along a West Coast, South Island, river system. *New Zealand Journal of Marine and Freshwater Research* 18: 379-388.

Winterbourn, M.J. & Fegley, A. (1989). Effects of nutrient enrichment and grazing on periphyton assemblages in some spring-fed, South Island streams. *New Zealand Natural Sciences* 16: 57-65.

Winterbourn, M.J. & Gregson, K.L.D. (1989). Guide to the Aquatic Insects of New Zealand. Revised edition. Bulletin of the Entomological Society of New Zealand No. 9.

Winterbourn, M.J.; Rounick, J.S. & Cowie, B. (1981). Are New Zealand stream

ecosystems really different? *New Zealand Journal of Marine and Freshwater Research* 15: 321-328.

Wrona, F.J.; Calow, P.; Ford, I.; Baird, D.J. & Maltby, L. (1986). Estimating the abundance of stone-dwelling organisms: a new method. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 2025-2035.

Yodzis, P. (1978). Competition for space and the structure of ecological communities. Lecture Notes in Biomathematics Vol. 25. Springer-Verlag, New York.

Yodzis, P. (1980). The connectance of real ecosystems. *Nature* 284: 544-545.

Zaret, T.M. & Rand, A.S. (1971). Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 54: 788-797.

Zaret, T.M. & Smith, E.P. (1984). On measuring niches and not measuring them. In *Evolutionary Ecology of Neotropical Freshwater Fishes* (ed. T.M. Zaret), pp. 127-137. W. Junk, The Hague.

Zipf, G.K. (1949). *Human Behaviour and the Principle of Least Effort*. Hafner, New York.

APPENDICES

APPENDIX I

DENSITY DATA FOR ALL STUDY SITES

Mean density (± 1 SE) per 0.1 m^2, of invertebrates collected in the five seasonal samples and the overall average of these densities, at each of the study sites. Densities are calculated using the technique of Wrona *et al.* (1986) (see Chapter 4), whereas number of species and total number of individuals are the numbers actually found on the fifteen collected stones taken in each season.

KOWAI RIVER

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Hydridae sp. A	0	0	0	2	0	0.4
	-	-	-	(2.1)	-	(0.4)
Neppia montana	0	0	0	2	0	0.4
	-	-	-	(2.1)	-	(0.4)
Nematoda sp. A	2	0	0	7	0	1.8
	(2.1)	-	-	(7.1)	-	(1.4)
Slavina sp.	13	8	15	23	0	11.8
	(4.0)	(7.2)	(8.4)	(9.4)	-	(3.8)
Eiseniella sp.	0	0	1	0	0	0.1
	-	-	(0.7)	-	-	(0.1)
Tardigrada sp. A	0	0	0	3	1	0.7
	-	-	-	(2.2)	(0.7)	(0.5)
Chydoridae sp.	0	0	0	2	0	0.4
	-	-	-	(2.1)	-	(0.4)
Ostracoda sp. A	1	0	2	2	0	1.0
	(0.7)	-	(2.1)	(2.1)	-	(0.5)
Harpacticoid Copepoda	0	0	0	3	0	0.7
	-	-	-	(2.3)	-	(0.7)
Cyclopoid Copepoda	0	0	0	0	2	0.4
	-	-	-	-	(2.1)	(0.4)
Collembola	18	0	5	68	13	20.7
	(9.1)	-	(2.7)	(13.4)	(7.6)	(12.3)
Nesameletus sp.	0	1	9	1	0	2.1
	-	(0.7)	(7.3)	(0.7)	-	(1.8)
Deleatidium sp. (*myzobranchia*-group)	354	357	427	44	525	341.4
	(72.9)	(66.7)	(81.0)	(10.8)	(71.1)	(80.6)
Zelandoperla decorata	8	17	21	3	0	9.8
	(7.2)	(8.4)	(8.3)	(2.2)	-	(4.0)
Zelandobius furcillatus	9	7	237	9	2	52.8
	(4.1)	(3.1)	(52.6)	(3.0)	(2.1)	(46.1)
Zelandobius unicolor	0	0	0	1	0	0.1
	-	-	-	(0.7)	-	(0.1)
Zelandobius pilosus	0	4	0	0	0	0.8
	-	(2.6)	-	-	-	(0.8)
Hydraenidae larvae sp. A	0	0	2	0	0	0.4
	-	-	(2.1)	-	-	(0.4)

Elmidae larvae sp. A	0	0	1	0	0	0.3
	-	-	(0.8)	-	-	(0.3)
Aphrophila neozelandica	0	0	2	0	0	0.4
	-	-	(2.1)	-	-	(0.4)
Eriopterini sp.	5	1	1	0	1	1.5
	(3.4)	(0.7)	(1.4)	-	(0.7)	(0.8)
Psychodidae	0	0	0	1	0	0.3
	-	-	-	(1.4)	-	(0.3)
Austrosimulium albovelatum	2243	32	84	0	18	475.4
	(404.0)	(14.9)	(23.9)	-	(14.4)	(442.1)
Macropelopiini sp.	20	0	0	3	0	4.5
	(7.0)	-	-	(2.2)	-	(3.8)
Parochlus sp. A	0	1	0	0	0	0.1
	-	(0.7)	-	-	-	(0.1)
Parochlus sp. B	72	0	0	0	2	14.8
	(15.7)	-	-	-	(2.1)	(14.3)
Maoridiamesa harrisi	1289	5	19	2	63	275.5
	(174.3)	(4.3)	(8.5)	(1.4)	(27.2)	(253.6)
Diamesinae sp. B	0	0	0	4	0	0.8
	-	-	-	(2.6)	-	(0.8)
Paucispinigera sp.	0	0	0	1	0	0.3
	-	-	-	(0.8)	-	(0.3)
Polypedilum sp.	2	0	0	0	2	0.8
	(1.4)	-	-	-	(2.1)	(0.5)
Tanytarsus vespertinus	11	43	11	11	45	24.2
	(7.5)	(42.8)	(7.6)	(7.6)	(21.0)	(8.1)
?*Rheocricotopus* sp.	137	37	251	14	10	89.6
	(28.3)	(28.9)	(97.3)	(4.8)	(7.5)	(46.4)
Orthocladiinae sp. B	0	0	11	0	0	2.1
	-	-	(7.5)	-	-	(2.1)
Orthocladiinae sp. A	0	0	0	0	2	0.4
	-	-	-	-	(2.1)	(0.4)
Orthocladiinae sp. C	0	0	0	0	1	0.1
	-	-	-	-	(0.7)	(0.1)
Eukiefferiella claripennis	1077	57	304	27	694	431.6
	(156.8)	(35.1)	(55.1)	(9.1)	(144.8)	(200.7)
Eukiefferiella sp. B	0	0	0	0	20	3.9
	-	-	-	-	(9.5)	(3.9)
Eukiefferiella sp. A	0	0	0	0	8	1.6
	-	-	-	-	(7.2)	(1.6)
Cricotopus aucklandensis	0	0	3	3	0	1.3
	-	-	(2.2)	(2.3)	-	(0.8)
Nothodixa sp.	0	0	0	3	0	0.5
	-	-	-	(2.2)	-	(0.5)
Empididae sp. A	5	8	0	0	9	4.5
	(3.0)	(7.2)	-	-	(7.4)	(1.9)
Ephydridae ?	11	0	0	0	0	2.2
	(5.9)	-	-	-	-	(2.2)
Limnophora sp. A	7	0	0	0	0	1.4
	(2.7)	-	-	-	-	(1.4)
Diptera indet.	0	0	0	1	0	0.1
	-	-	-	(0.7)	-	(0.1)
Plectrocnemia maclachlani	0	4	0	0	3	1.5
	-	(4.2)	-	-	(2.3)	(0.9)
Aoteapsyche colonica	0	11	1	0	0	2.5
	-	(7.6)	(0.8)	-	-	(2.2)

Aoteapsyche rarurarv	0	0	3	0	0	0.5
	-	-	(2.2)	-	-	(0.5)
Hydrobiosis parumbripennis	2	0	0	0	0	0.4
	(0.9)	-	-	-	-	(0.4)
Hydrobiosis harpidiosa	3	1	0	0	0	0.7
	(2.2)	(0.7)	-	-	-	(0.5)
Hydrobiosis spatulata	0	0	5	0	0	1.1
	-	-	(2.8)	-	-	(1.1)
Psilochorema bidens	2	3	7	0	2	2.7
	(0.9)	(1.3)	(2.9)	-	(1.4)	(1.1)
Hydrochorema tenuicaudatum	0	0	0	2	0	0.4
	-	-	-	(2.1)	-	(0.4)
Costachorema brachyptera	2	0	0	0	0	0.4
	(2.1)	-	-	-	-	(0.4)
early instar Hydrobiosidae	14	34	31	1	1	16.3
	(5.0)	(10.8)	(11.0)	(0.8)	(0.7)	(7.2)
Oxyethira albiceps	0	3	4	0	0	1.3
	-	(2.2)	(1.8)	-	-	(0.8)
Oeconesus maori ?	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Pycnocentrodes sp.	1	0	0	0	1	0.4
	(0.7)	-	-	-	(0.8)	(0.3)
Beraeoptera roria	0	0	3	0	0	0.7
	-	-	(2.3)	-	-	(0.7)
Olinga feredayi	0	0	0	0	2	0.4
	-	-	-	-	(2.1)	(0.4)
Oribatei sp. A	1	0	0	4	0	1.0
	(0.7)	-	-	(4.2)	-	(0.8)
Notoaturinae sp. A	7	13	50	0	53	24.6
	(2.8)	(6.2)	(15.0)	-	(26.3)	(11.3)
parasitic mite	0	0	0	0	1	0.1
	-	-	-	-	(0.7)	(0.1)
pupae	35	1	25	0	2	12.7
	(10.2)	(0.8)	(9.2)	-	(2.1)	(7.3)
Number of species	28	21	27	28	25	25.8
						(1.3)
Total number of individuals	3217	345	932	184	638	1063.2
						(553.4)

WHITEWATER STREAM

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Hydridae sp. A	0	0	1	0	0	0.1
	-	-	(0.7)	-	-	(0.1)
Hydridae sp. B	0	2	0	0	0	0.4
	-	(2.0)	-	-	-	(0.4)
Neppia montana	14	5	11	1	5	7.1
	(4.6)	(2.5)	(5.0)	(0.7)	(5.0)	(2.5)
Spathula sp.	0	0	1	0	0	0.1
	-	-	(0.7)	-	-	(0.1)
Rhabdocoela	0	3	4	0	0	1.4
	-	(3.4)	(3.9)	-	-	(0.9)
Nematoda sp. A	0	0	2	0	3	0.9
	-	-	(2.0)	-	(2.1)	(0.6)
Potamopyrgus antipodarum	0	1	1	1	0	0.4
	-	(0.7)	(0.7)	(0.7)	-	(0.2)
Slavina sp.	169	66	166	9	0	82.0
	(44.5)	(21.8)	(53.1)	(2.9)	-	(36.8)
Eiseniella sp.	0	1	2	0	1	0.7
	-	(0.7)	(2.0)	-	(0.7)	(0.4)
Lumbriculus variegatus	4	0	0	0	0	0.8
	(2.4)	-	-	-	-	(0.8)
Oligocheata sp.	0	0	1	0	0	0.1
	-	-	(0.7)	-	-	(0.1)
Chydoridae sp.	1	0	9	1	0	2.0
	(0.7)	-	(5.5)	(0.7)	-	(1.7)
Ostracoda sp. A	0	1	1	0	0	0.3
	-	(0.7)	(0.7)	-	-	(0.2)
Harpacticoid Copepoda	6	5	29	3	0	8.7
	(4.0)	(2.5)	(8.8)	(2.1)	-	(5.3)
Collembola	11	24	9	42	5	18.2
	(6.3)	(9.8)	(5.4)	(8.4)	(2.6)	(6.7)
Nesameletus sp.	5	0	0	0	0	0.9
	(2.6)	-	-	-	-	(0.9)
Deleatidium sp. (*myzobranchia*-group)	1715	735	125	343	129	609.3
	(246.2)	(121.3)	(23.4)	(95.6)	(20.5)	(297.9)
Stenoperla maclellani	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Zelandoperla decorata	9	6	2	0	0	3.5
	(5.8)	(5.9)	(1.4)	-	-	(1.8)
Zelandobius furcillatus	4	3	14	1	0	4.3
	(2.4)	(2.1)	(10.2)	(0.7)	-	(2.6)
Zelandobius unicolor	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Zelandobius pilosus	5	4	10	0	0	3.9
	(2.9)	(2.2)	(6.1)	-	-	(1.9)
Zelandobius sp.	0	2	0	0	0	0.4
	-	(2.0)	-	-	-	(0.4)
Archichauliodes diversus	0	11	1	0	0	2.4
	-	(6.4)	(0.8)	-	-	(2.1)
Elmidae larvae sp. A	15	49	30	0	3	19.3
	(7.1)	(16.9)	(11.1)	-	(2.1)	(9.1)
Elmidae larvae sp. B	0	11	0	0	0	2.1
	-	(7.7)	-	-	-	(2.1)

Neocurupira hudsoni-complex	0	0	0	2	0	0.4
	-	-	-	(0.9)	-	(0.4)
Aphrophila neozelandica	2	5	1	1	1	2.0
	(0.9)	(5.0)	(0.8)	(0.8)	(0.7)	(0.7)
Eriopterini sp.	6	5	15	3	1	6.1
	(2.6)	(2.4)	(10.0)	(2.4)	(0.7)	(2.5)
Hexatomini sp.	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Paralimnophila sp.	1	0	0	0	0	0.3
	(1.4)	-	-	-	-	(0.3)
Austrosimulium albovelatum	114	53	35	7	4	42.8
	(27.0)	(25.0)	(10.5)	(4.1)	(2.8)	(20.1)
Macropelopiini sp.	1	0	0	1	0	0.3
	(0.7)	-	-	(0.7)	-	(0.2)
Parochlus sp. A	2	2	0	1	0	0.9
	(2.0)	(2.0)	-	(0.7)	-	(0.4)
Maoridiamesa harrisi	55	48	118	376	13	122.0
	(18.4)	(15.9)	(48.5)	(290.4)	(10.4)	(65.7)
Tanytarsus vespertinus	91	5	10	5	12	24.6
	(33.9)	(5.0)	(9.9)	(4.7)	(10.2)	(16.8)
?Rheocricotopus sp.	52	38	286	14	0	78.0
	(20.0)	(14.7)	(136.3)	(5.5)	-	(52.8)
Orthocladiinae sp. B	10	41	0	0	0	10.3
	(6.2)	(12.4)	-	-	-	(7.9)
Eukiefferiella claripennis	254	49	165	32	11	102.0
	(58.5)	(16.9)	(66.1)	(19.5)	(5.9)	(46.4)
Cricotopus aucklandensis	0	2	139	33	8	36.4
	-	(2.0)	(53.2)	(12.2)	(5.4)	(26.3)
Empididae sp. A	1	1	0	0	5	1.2
	(0.7)	(0.7)	-	-	(5.0)	(0.9)
Aoteapsyche colonica	42	55	36	6	0	27.7
	(11.8)	(21.1)	(12.7)	(2.6)	-	(10.6)
Aoteapsyche raruraru	0	120	22	9	0	30.1
	-	(26.0)	(21.6)	(5.6)	-	(22.7)
Hydrobiosis parumbripennis	1	1	0	3	0	0.9
	(0.7)	(1.4)	-	(2.1)	-	(0.5)
Hydrobiosis spatulata	0	2	0	0	0	0.4
	-	(2.0)	-	-	-	(0.4)
Psilochorema bidens	26	4	2	1	1	6.7
	(8.8)	(2.0)	(2.0)	(0.7)	(0.7)	(4.9)
Costachorema callista	0	1	2	0	0	0.5
	-	(0.7)	(2.0)	-	-	(0.4)
Costachorema xanthoptera	0	4	0	1	0	0.9
	-	(2.4)	-	(0.7)	-	(0.8)
early instar Hydrobiosidae	17	27	60	13	5	24.2
	(7.6)	(8.3)	(15.9)	(5.9)	(5.0)	(9.6)
Oxyethira albiceps	0	0	0	1	0	0.1
	-	-	-	(0.7)	-	(0.1)
Zelolessica cheira	0	0	5	0	0	1.0
	-	-	(5.0)	-	-	(1.0)
Pycnocentrodes sp.	33	10	1	1	0	9.1
	(13.9)	(5.5)	(0.7)	(0.8)	-	(6.3)
Beraeoptera roria	7	1	1	0	0	2.0
	(3.1)	(0.8)	(0.8)	-	-	(1.3)
Olinga feredayi	17	11	26	5	0	11.8
	(4.8)	(3.3)	(11.1)	(2.7)	-	(4.5)

Oribatei sp. A	0	1	0	0	0	0.1
	-	(0.7)	-	-	-	(0.1)
Hydrachenellae sp. A	2	0	0	0	1	0.5
	(1.4)	-	-	-	(0.7)	(0.4)
Notoaturinae sp. A	166	147	149	5	1	93.8
	(27.2)	(33.0)	(35.9)	(4.0)	(0.7)	(37.2)
parasitic mite	16	0	1	0	0	3.4
	(15.7)	-	(1.4)	-	-	(3.0)
pupae	5	3	65	3	1	15.3
	(2.4)	(1.9)	(38.8)	(2.6)	(0.7)	(12.4)
Number of species	37	41	38	29	18	32.6
						(4.2)
Total number of individuals	1991	1083	880	1047	134	1027
						(296.0)

DRY STREAM

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Hydridae sp. A	1	0	24	1	0	5.0
	(0.6)	-	(8.7)	(0.6)	-	(4.7)
Hydridae sp. B	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)
Neppia montana	2	1	2	0	0	1.0
	(1.3)	(0.8)	(1.3)	-	-	(0.4)
Rhabdocoela	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)
Nematoda sp. A	0	0	0	1	2	0.5
	-	-	-	(0.6)	(1.9)	(0.4)
Potamopyrgus antipodarum	0	0	2	0	0	0.4
	-	-	(1.9)	-	-	(0.4)
Slavina sp.	141	345	37	3	0	105.0
	(36.4)	(67.4)	(12.2)	(2.0)	-	(65.2)
Eiseniella sp.	0	0	83	0	1	16.6
	-	-	(25.4)	-	(0.6)	(16.5)
Tardigrada sp. A	0	4	1	0	0	0.9
	-	(2.3)	(0.6)	-	-	(0.7)
Harpacticoid Copepoda	2	19	11	1	1	6.7
	(1.9)	(6.8)	(6.7)	(0.6)	(0.6)	(3.7)
Paraleptamphopus subterraneus	0	0	0	0	2	0.4
	-	-	-	-	(1.9)	(0.4)
Collembola	49	16	0	29	4	19.7
	(35.8)	(5.6)	-	(7.6)	(3.9)	(8.9)
Nesameletus sp.	0	7	14	2	0	4.4
	-	(4.5)	(5.7)	(1.9)	-	(2.6)
Deleatidium sp. (*myzobranchia*-group)	639	611	1029	323	229	566.3
	(101.8)	(110.0)	(186.3)	(56.8)	(51.3)	(140.5)
Stenoperla maclellani	0	1	0	1	0	0.2
	-	(0.6)	-	(0.6)	-	(0.1)
Zelandoperla decorata	4	6	2	10	0	4.5
	(1.4)	(4.0)	(1.9)	(2.9)	-	(1.8)
Zelandobius furcillatus	11	15	12	3	2	8.7
	(5.7)	(8.5)	(3.6)	(1.8)	(1.9)	(2.7)
Zelandobius unicolor	0	0	4	0	0	0.8
	-	-	(3.8)	-	-	(0.8)
Zelandobius pilosus	0	91	18	1	0	22.0
	-	(23.7)	(6.5)	(0.6)	-	(17.6)
Staphylinidae	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)
Orchymontia spinipennis	0	4	0	4	1	1.7
	-	(4.0)	-	(4.0)	(0.6)	(0.9)
Scirtidae sp. B	1	0	0	0	0	0.1
	(0.6)	-	-	-	-	(0.1)
Elmidae larvae sp. A	11	33	27	1	7	15.7
	(4.5)	(12.0)	(12.0)	(0.6)	(2.9)	(6.2)
Elmidae larvae sp. B	0	73	0	0	0	14.6
	-	(21.0)	-	-	-	(14.6)
Aphrophila neozelandica	10	1	0	4	0	3.0
	(5.4)	(0.6)	-	(1.4)	-	(1.9)
Eriopterini sp.	0	0	0	1	0	0.1
	-	-	-	(0.6)	-	(0.1)

Paralimnophila sp.	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)
Ceratopogonidae	0	0	1	0	0	0.1
	-	-	(0.6)	-	-	(0.1)
Austrosimulium albovelatum	120	33	0	2	19	34.7
	(44.5)	(13.1)	-	(1.9)	(8.9)	(22.1)
Thaumaleidae	0	0	1	0	0	0.1
	-	-	(0.6)	-	-	(0.1)
Macropelopiini sp.	0	0	1	0	0	0.1
	-	-	(0.6)	-	-	(0.1)
Parochlus sp. A	1	0	0	0	5	1.0
	(0.6)	-	-	-	(4.1)	(0.9)
Parochlus sp. B	15	4	0	0	0	3.7
	(5.8)	(2.7)	-	-	-	(2.8)
Maoridiamesa harrisi	20	88	3	0	114	44.8
	(10.1)	(22.0)	(2.0)	-	(39.8)	(23.6)
Paucispinigera sp.	8	0	1	0	0	1.7
	(4.6)	-	(0.6)	-	-	(1.5)
Tanytarsus vespertinus	72	36	131	27	25	58.3
	(20.6)	(17.9)	(48.2)	(24.4)	(13.1)	(20.1)
?*Rheocricotopus* sp.	246	500	111	2	38	179.2
	(90.0)	(108.9)	(31.3)	(1.3)	(17.1)	(90.4)
Orthocladiinae sp. B	0	11	18	0	3	6.1
	-	(3.8)	(6.1)	-	(2.0)	(3.4)
Eukiefferiella claripennis	593	201	12	13	76	178.7
	(141.7)	(37.3)	(4.7)	(5.8)	(16.3)	(109.1)
Eukiefferiella sp. A	0	0	0	0	4	0.8
	-	-	-	-	(2.4)	(0.8)
Cricotopus aucklandensis	0	23	3	2	24	10.4
	-	(6.5)	(2.1)	(1.9)	(6.5)	(5.4)
Empididae sp. A	18	42	1	0	0	12.2
	(9.5)	(16.5)	(0.8)	-	-	(8.2)
Ephydridae ?	0	2	0	0	0	0.4
	-	(1.9)	-	-	-	(0.4)
Limnophora sp. A	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)
Polyplectropus puerilis	0	1	4	0	0	0.9
	-	(0.6)	(4.0)	-	-	(0.8)
Aoteapsyche colonica	26	12	33	24	1	19.3
	(7.7)	(4.7)	(21.4)	(6.9)	(0.6)	(5.7)
Aoteapsyche raruraru	0	0	0	4	0	0.7
	-	-	-	(2.7)	-	(0.7)
Hydrobiosis parumbripennis	4	5	5	1	0	3.1
	(2.3)	(2.0)	(2.5)	(0.6)	-	(1.1)
Hydrobiosis clavigera	6	2	0	0	0	1.5
	(4.0)	(1.9)	-	-	-	(1.1)
Hydrobiosis sp.	4	1	0	0	0	0.9
	(2.4)	(0.6)	-	-	-	(0.7)
Psilochorema bidens	13	11	24	2	1	10.0
	(5.6)	(4.9)	(8.0)	(1.3)	(0.6)	(4.3)
Psilochorema nemorale	0	0	3	0	0	0.5
	-	-	(2.0)	-	-	(0.5)
Psilochorema leptoharpax	1	0	0	0	0	0.1
	(0.6)	-	-	-	-	(0.1)
Costachorema brachyptera	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)

Costachorema callista	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)
Costachorema xanthoptera	1	0	0	0	0	0.2
	(0.8)	-	-	-	-	(0.2)
Neurochorema confusum	0	0	0	0	2	0.4
	-	-	-	-	(1.9)	(0.4)
early instar Hydrobiosidae	39	59	32	2	1	26.3
	(12.7)	(13.2)	(8.7)	(1.3)	(0.6)	(11.2)
Oxyethira albiceps	0	23	0	0	0	4.7
	-	(9.6)	-	-	-	(4.7)
Hudsonema amabilis	0	0	10	0	0	2.0
	-	-	(8.3)	-	-	(2.0)
Zelolessica cheira	1	0	28	1	0	6.0
	(0.6)	-	(6.5)	(1.2)	-	(5.5)
Pycnocentrodes sp.	9	11	295	32	0	69.4
	(8.1)	(5.9)	(75.7)	(9.8)	-	(56.7)
Beraeoptera roria	15	38	167	87	2	61.9
	(7.8)	(13.5)	(29.6)	(67.1)	(1.2)	(30.0)
Olinga feredayi	1	7	20	3	0	6.0
	(0.6)	(4.2)	(6.5)	(2.3)	-	(3.6)
Oribatei sp. A	1	0	0	0	2	0.5
	(0.6)	-	-	-	(1.9)	(0.4)
Hydrachenellae sp. A	1	8	7	3	0	3.5
	(0.6)	(4.5)	(4.5)	(2.0)	-	(1.6)
Notoaturinae sp. A	12	62	67	1	11	30.4
	(5.9)	(21.7)	(28.2)	(0.6)	(5.8)	(14.0)
Hydrachenellae sp. C	1	1	0	0	0	0.4
	(0.8)	(0.6)	-	-	-	(0.2)
parasitic mite	0	0	0	4	0	0.7
	-	-	-	(3.7)	-	(0.7)
pupae	40	23	20	0	4	17.5
	(14.3)	(6.7)	(7.9)	-	(2.3)	(7.2)
Number of species	36	46	38	32	25	(35.4)
						(3.5)
Total number of individuals	1557	2270	1790	572	474	1332.6
						(350.3)

CRAIGIEBURN CUTTING STREAM

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Neppia montana	93	33	70	1	20	43.3
	(32.0)	(6.7)	(25.5)	(0.8)	(10.5)	(16.7)
Nematoda sp. A	1	3	0	0	0	1.0
	(1.0)	(2.2)	-	-	-	(0.7)
Gordius sp.	0	1	0	0	0	0.1
	-	(0.8)	-	-	-	(0.1)
Slavina sp.	35	26	76	6	2	29.0
	(12.2)	(11.6)	(26.1)	(3.0)	(2.0)	(13.2)
Eiseniella sp.	0	0	0	0	3	0.6
	-	-	-	-	(2.3)	(0.6)
Ostracoda sp. A	4	3	12	0	2	4.0
	(4.0)	(2.1)	(11.0)	-	(2.0)	(2.0)
Ostracoda sp. B	2	0	0	0	0	0.4
	(1.6)	-	-	-	-	(0.4)
Harpacticoid Copepoda	21	12	39	3	0	14.8
	(5.1)	(4.9)	(14.5)	(2.1)	-	(7.0)
Collembola	28	0	7	2	5	8.4
	(16.2)	-	(4.1)	(2.0)	(2.7)	(5.0)
Microchorista philpotti	0	2	0	0	0	0.4
	-	(2.0)	-	-	-	(0.4)
Coloburiscus humeralis	0	0	1	0	0	0.1
	-	-	(0.8)	-	-	(0.1)
Nesameletus sp.	48	66	50	1	0	33.0
	(18.5)	(18.6)	(13.8)	(0.8)	-	(13.6)
Deleatidium sp. (*myzobranchia*-group)	457	233	317	47	19	214.6
	(78.4)	(51.1)	(65.5)	(11.5)	(8.2)	(82.4)
Stenoperla maclellani	0	3	2	0	0	1.0
	-	(2.1)	(1.0)	-	-	(0.6)
Zelandoperla decorata	0	0	1	0	0	0.1
	-	-	(0.8)	-	-	(0.1)
Zelandobius furcillatus	24	0	11	0	0	7.0
	(8.8)	-	(10.9)	-	-	(4.8)
Zelandobius pilosus	3	0	0	0	0	0.5
	(2.1)	-	-	-	-	(0.5)
Spaniocerca zelandica	135	5	39	2	1	36.5
	(31.9)	(5.5)	(10.1)	(2.0)	(1.0)	(25.6)
Staphylinidae	4	0	0	5	0	1.9
	(2.5)	-	-	(5.5)	-	(1.2)
Orchymontia spinipennis	21	9	7	2	0	7.7
	(8.0)	(6.0)	(3.2)	(2.0)	-	(3.7)
Homalaena spatulata	0	6	1	2	1	2.0
	-	(5.5)	(1.0)	(2.0)	(0.8)	(1.1)
Hydraenidae larvae sp. A	0	1	0	0	0	0.1
	-	(0.8)	-	-	-	(0.1)
Hydraenidae larvae sp. B	0	2	0	0	0	0.4
	-	(2.0)	-	-	-	(0.4)
Scirtidae sp. A	0	0	0	1	0	0.1
	-	-	-	(0.8)	-	(0.1)
Elmidae larvae sp. A	15	3	13	0	0	6.0
	(7.1)	(1.0)	(7.0)	-	-	(3.2)
Peritheates turrifer	0	0	0	0	1	0.1
	-	-	-	-	(0.8)	(0.1)

Eriopterini sp.	0	2	0	0	3	0.9
	-	(2.0)	-	-	(2.1)	(0.6)
?*Molophilus* sp.	0	0	0	1	0	0.1
	-	-	-	(0.8)	-	(0.1)
Ceratopogonidae	9	1	2	4	0	3.1
	(6.0)	(0.8)	(2.0)	(4.0)	-	(1.6)
Austrosimulium albovelatum	48	45	21	0	3	23.3
	(11.2)	(19.0)	(8.2)	-	(2.1)	(10.1)
Macropelopiini sp.	17	0	1	1	0	3.7
	(6.2)	-	(0.8)	(0.8)	-	(3.4)
Parochlus sp. B	3	1	0	0	0	0.7
	(2.1)	(0.8)	-	-	-	(0.5)
Podonomus sp.	0	1	0	0	0	0.3
	-	(1.5)	-	-	-	(0.3)
Maoridiamesa harrisi	27	11	1	1	0	7.8
	(11.2)	(10.9)	(0.8)	(0.8)	-	(5.2)
Paucispinigera sp.	25	26	70	1	0	24.3
	(7.9)	(12.1)	(25.4)	(0.8)	-	(12.7)
Tanytarsus vespertinus	0	0	0	1	0	0.1
	-	-	-	(0.8)	-	(0.1)
?*Cladopelma* sp.	0	31	3	0	1	6.8
	-	(10.4)	(2.1)	-	(0.8)	(6.0)
?*Rheocricotopus* sp.	63	136	29	1	0	45.8
	(16.9)	(70.6)	(9.8)	(0.8)	-	(25.4)
Orthocladiinae sp. B	0	0	0	1	0	0.1
	-	-	-	(0.8)	-	(0.1)
Orthocladiinae sp. C	0	0	1	0	0	0.1
	-	-	(0.8)	-	-	(0.1)
Eukiefferiella claripennis	28	19	5	0	1	10.8
	(8.3)	(11.4)	(5.5)	-	(1.0)	(5.5)
Cricotopus aucklandensis	0	0	1	0	0	0.1
	-	-	(0.8)	-	-	(0.1)
Nothodixa sp.	1	2	6	0	0	1.6
	(0.8)	(2.0)	(2.5)	-	-	(1.0)
Empididae sp. A	0	0	2	0	0	0.4
	-	-	(2.0)	-	-	(0.4)
Empididae sp. B	28	38	22	1	0	17.7
	(9.6)	(17.1)	(12.2)	(0.8)	-	(7.5)
Ephydridae ?	3	0	0	0	0	0.5
	(2.1)	-	-	-	-	(0.5)
Diptera indet.	0	0	0	4	1	0.9
	-	-	-	(4.0)	(0.8)	(0.8)
Hydrobiosella stenocerca	0	3	0	0	0	0.7
	-	(2.2)	-	-	-	(0.7)
Polyplectropus puerilis	0	0	0	1	0	0.1
	-	-	-	(0.8)	-	(0.1)
Aoteapsyche colonica	0	8	0	0	0	1.6
	-	(5.9)	-	-	-	(1.6)
Aoteapsyche rarurarn	0	0	12	0	0	2.4
	-	-	(6.2)	-	-	(2.4)
Hydrobiosis harpidiosa	0	0	1	0	0	0.1
	-	-	(0.8)	-	-	(0.1)
Hydrobiosis spatulata	7	1	0	0	0	1.5
	(3.2)	(0.8)	-	-	-	(1.3)
Psilochorema bidens	1	1	0	0	0	0.3
	(0.8)	(0.8)	-	-	-	(0.2)

Psilochorema nemorale	1	0	0	0	0	0.1
	(0.8)	-	-	-	-	(0.1)
Psilochorema tautoru	0	0	10	0	0	2.1
	-	-	(5.8)	-	-	(2.1)
Hydrochorema tenuicaudatum	1	0	0	0	0	0.1
	(0.8)	-	-	-	-	(0.1)
Costachorema brachyptera	0	1	0	0	0	0.1
	-	(0.8)	-	-	-	(0.1)
Costachorema callista	2	0	0	0	0	0.4
	(1.6)	-	-	-	-	(0.4)
early instar Hydrobiosidae	9	15	20	0	0	8.7
	(2.8)	(7.1)	(7.1)	-	-	(4.0)
Zelandopsyche ingens	0	5	0	0	0	0.9
	-	(4.1)	-	-	-	(0.9)
Oeconesidae indet.	3	0	0	1	0	0.7
	(2.1)	-	-	(0.8)	-	(0.5)
Philorheithrus agilis	10	16	21	2	0	9.8
	(4.0)	(8.4)	(6.4)	(2.0)	-	(4.1)
Zelolessica cheira	1	0	0	0	0	0.1
	(0.8)	-	-	-	-	(0.1)
Pycnocentrodes sp.	1	0	8	0	0	1.8
	(0.8)	-	(5.9)	-	-	(1.6)
Olinga feredayi	7	6	6	1	2	4.2
	(4.1)	(5.2)	(2.7)	(0.8)	(2.0)	(1.2)
Oribatei sp. A	9	1	0	0	0	1.9
	(5.9)	(0.8)	-	-	-	(1.7)
Hydrachenellae sp. A	3	4	8	0	0	2.9
	(2.3)	(2.5)	(5.7)	-	-	(1.4)
Notoaturinae sp. A	10	25	30	1	0	13.2
	(4.7)	(8.2)	(10.0)	(0.8)	-	(6.2)
Hydrachenellae sp. C	2	0	0	0	0	0.4
	(2.0)	-	-	-	-	(0.4)
Notoaturinae sp. D	0	0	1	0	0	0.1
	-	-	(0.8)	-	-	(0.1)
pupae	5	7	2	0	0	2.7
	(2.5)	(3.4)	(2.0)	-	-	(1.3)
Number of species	41	40	38	26	15	32.0
						(5.0)
Total number of individuals	878	452	571	66	62	405.8
						(155.9)

BRUCE STREAM

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Nematoda sp. A	0	2	0	0	8	2.0
	-	(2.0)	-	-	(4.0)	(1.5)
Slavina sp.	15	3	0	2	0	3.8
	(4.8)	(2.1)	-	(2.0)	-	(2.7)
Eiseniella sp.	0	0	0	0	7	1.3
	-	-	-	-	(4.0)	(1.3)
Chydoridae sp.	0	0	1	0	0	0.1
	-	-	(0.7)	-	-	(0.1)
Harpacticoid Copepoda	1	4	0	0	0	0.8
	(0.7)	(3.5)	-	-	-	(0.7)
Collembola	8	0	2	0	5	2.8
	(3.1)	-	(2.0)	-	(2.8)	(1.5)
Nesameletus sp.	2	0	0	0	0	0.4
	(2.0)	-	-	-	-	(0.4)
Deleatidium sp.						
(*myzobranchia*-group)	96	133	267	11	16	104.6
	(24.6)	(24.4)	(43.3)	(4.5)	(8.2)	(46.8)
Zelandoperla decorata	10	18	58	0	0	17.3
	(3.8)	(5.0)	(15.2)	-	-	(10.8)
Zelandobius furcillatus	7	4	14	2	2	5.8
	(4.3)	(3.9)	(7.4)	(2.0)	(2.0)	(2.3)
Zelandobius indet.	12	0	0	0	0	2.5
	(7.3)	-	-	-	-	(2.5)
Megaleptoperla grandis	0	5	0	0	0	1.0
	-	(4.0)	-	-	-	(1.0)
Staphylinidae	0	0	0	0	2	0.4
	-	-	-	-	(2.0)	(0.4)
Scirtidae sp. B	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Elmidae larvae sp. A	0	0	3	0	0	0.6
	-	-	(2.1)	-	-	(0.6)
Neocurupira campbelli	1	1	0	0	0	0.3
	(0.7)	(0.7)	-	-	-	(0.2)
Peritheates turrifer	0	0	2	0	0	0.4
	-	-	(2.0)	-	-	(0.4)
Eriopterini sp.	0	1	0	0	0	0.1
	-	(0.7)	-	-	-	(0.1)
Ceratopogonidae	2	0	0	0	0	0.4
	(2.0)	-	-	-	-	(0.4)
Austrosimulium albovelatum	5	38	2	0	0	8.9
	(2.3)	(11.7)	(2.0)	-	-	(7.3)
Parochlus sp. A	2	0	0	0	0	0.4
	(2.0)	-	-	-	-	(0.4)
Parochlus sp. B	26	0	0	0	0	5.2
	(9.2)	-	-	-	-	(5.2)
Maoridiamesa harrisi	0	1	0	0	0	0.1
	-	(0.7)	-	-	-	(0.1)
Paucispinigera sp.	0	0	5	2	2	1.8
	-	-	(2.5)	(2.0)	(2.0)	(1.0)
Polypedilum sp.	0	1	0	0	0	0.1
	-	(0.7)	-	-	-	(0.1)
Tanytarsus vespertinus	7	0	1	0	0	1.6
	(4.0)	-	(0.7)	-	-	(1.4)

?*Rheocricotopus* sp.	22	13	4	3	1	8.6
	(7.5)	(5.4)	(3.9)	(2.1)	(0.7)	(4.1)
Orthocladiinae sp. C	8	0	0	0	0	1.7
	(7.9)	-	-	-	-	(1.7)
Eukiefferiella claripennis	9	11	13	0	0	6.7
	(4.4)	(5.1)	(5.2)	-	-	(2.8)
Cricotopus aucklandensis	0	0	2	0	0	0.4
	-	-	(2.0)	-	-	(0.4)
Chironomidae indet.	0	0	0	0	2	0.4
	-	-	-	-	(2.0)	(0.4)
Empididae sp. B	0	0	0	4	0	0.7
	-	-	-	(3.5)	-	(0.7)
Ephydridae ?	2	0	0	0	0	0.4
	(2.0)	-	-	-	-	(0.4)
Diptera indet.	0	0	2	1	0	0.5
	-	-	(2.0)	(0.7)	-	(0.4)
Hydrobiosis sp.	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Costachorema callista	5	2	0	0	0	1.3
	(2.5)	(2.0)	-	-	-	(0.9)
early instar Hydrobiosidae	0	9	7	0	0	3.0
	-	(4.4)	(4.0)	-	-	(1.9)
Oxyethira albiceps	0	2	0	0	0	0.4
	-	(2.0)	-	-	-	(0.4)
Pycnocentrodes sp.	0	8	0	0	0	1.7
	-	(7.2)	-	-	-	(1.7)
Oribatei sp. A	0	0	0	0	1	0.1
	-	-	-	-	(0.7)	(0.1)
Notoaturinae sp. A	0	4	2	0	0	1.2
	-	(3.6)	(2.0)	-	-	(0.8)
parasitic mite	25	0	0	0	0	5.1
	(25.6)	-	-	-	-	(5.1)
pupae	3	0	2	0	0	0.9
	(2.1)	-	(2.0)	-	-	(0.6)
Number of species	22	19	16	7	10	14.8
						(2.8)
Total number of individuals	194	172	319	16	33	146.8
						(55.9)

PORTER RIVER

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Hydridae sp. A	14	13	81	75	0	36.5
	(5.4)	(4.4)	(18.1)	(18.9)	-	(17.1)
Hydridae sp. B	0	2	0	4	0	1.2
	-	(1.7)	-	(2.3)	-	(0.8)
Neppia montana	130	150	74	244	214	162.3
	(29.4)	(38.9)	(21.1)	(59.6)	(68.6)	(30.2)
Spathula sp.	0	1	6	0	2	1.8
	-	(0.8)	(3.7)	-	(1.6)	(1.2)
Rhabdocoela	9	16	20	9	2	11.2
	(5.1)	(7.0)	(9.0)	(5.0)	(1.7)	(3.2)
Nematoda sp. A	7	7	51	31	24	24.0
	(5.2)	(4.6)	(14.5)	(8.7)	(9.5)	(8.1)
Nematoda sp. B	0	0	0	0	3	0.6
	-	-	-	-	(2.3)	(0.6)
Potamopyrgus antipodarum	114	178	145	194	70	140.2
	(23.3)	(45.9)	(27.2)	(44.2)	(19.1)	(22.3)
Slavina sp.	188	168	1150	122	0	325.5
	(37.2)	(31.4)	(249.7)	(24.4)	-	(208.7)
Eiseniella sp.	0	0	0	0	62	12.4
	-	-	-	-	(17.1)	(12.4)
Tubificidae sp.	0	0	3	5	0	1.6
	-	-	(2.1)	(3.5)	-	(1.0)
Lumbriculus variegatus	4	1	1	0	0	1.1
	(2.4)	(0.8)	(0.8)	-	-	(0.7)
Oligocheata sp.	0	0	107	7	0	22.9
	-	-	(25.4)	(4.6)	-	(21.1)
Tardigrada sp. A	0	63	36	4	0	20.7
	-	(27.0)	(10.6)	(4.2)	-	(12.6)
Tardigrada sp. B	0	0	2	0	0	0.5
	-	-	(1.9)	-	-	(0.5)
Chydoridae sp.	2	2	35	12	1	10.5
	(1.9)	(1.7)	(16.6)	(5.3)	(0.8)	(6.5)
Ostracoda sp. A	15	20	7	9	0	10.1
	(5.0)	(5.2)	(3.6)	(3.7)	-	(3.5)
Harpacticoid Copepoda	730	2449	1814	403	66	1092.4
	(221.2)	(997.6)	(360.9)	(102.4)	(24.0)	(448.5)
Cyclopoid Copepoda	1	0	0	0	2	0.5
	(0.8)	-	-	-	(1.7)	(0.3)
Paraleptamphopus subterraneus	0	0	2	0	0	0.3
	-	-	(1.7)	-	-	(0.3)
Collembola	10	8	1	8	3	6.0
	(3.1)	(4.3)	(0.8)	(5.3)	(2.3)	(1.7)
Deleatidium sp. (*myzobranchia*-group)	426	521	920	786	666	663.5
	(72.8)	(102.6)	(161.3)	(94.7)	(111.0)	(88.7)
Stenoperla maclellani	1	2	3	0	0	1.1
	(0.8)	(1.0)	(2.1)	-	-	(0.6)
Zelandoperla decorata	2	6	4	13	1	5.1
	(1.6)	(3.6)	(2.3)	(12.1)	(0.8)	(2.2)
Zelandobius furcillatus	2	2	235	44	1	56.9
	(1.9)	(1.7)	(42.9)	(20.5)	(0.8)	(45.4)
Zelandobius unicolor	0	0	0	0	1	0.2
	-	-	-	-	(0.8)	(0.2)

Zelandobius pilosus	7	117	36	41	7	41.2
	(2.7)	(39.6)	(9.9)	(23.4)	(4.8)	(20.1)
Staphylinidae	2	0	0	0	0	0.3
	(1.7)	-	-	-	-	(0.3)
Orchymontia spinipennis	0	0	1	2	0	0.5
	-	-	(0.8)	(1.7)	-	(0.3)
Scirtidae sp. B	4	2	2	1	1	2.1
	(2.0)	(1.9)	(1.9)	(0.8)	(0.8)	(0.6)
Elmidae larvae sp. A	0	0	6	0	0	1.2
	-	-	(3.5)	-	-	(1.2)
Aphrophila neozelandica	8	6	29	7	7	11.6
	(4.8)	(3.2)	(8.5)	(4.6)	(2.7)	(4.5)
Limonia nigrescens	0	0	1	1	0	0.3
	-	-	(0.8)	(0.8)	-	(0.2)
Psychodidae	0	1	0	0	0	0.2
	-	(0.8)	-	-	-	(0.2)
Austrosimulium laticorne	1372	158	563	171	321	516.9
	(378.0)	(32.1)	(140.0)	(43.7)	(94.8)	(225.7)
Macropelopiini sp.	35	2	0	2	0	7.6
	(11.2)	(1.0)	-	(1.7)	-	(6.8)
Parochlus sp. A	150	61	7	2	1	44.1
	(74.9)	(23.8)	(2.8)	(1.0)	(0.8)	(28.7)
Parochlus sp. B	1	6	0	0	0	1.3
	(0.8)	(3.5)	-	-	-	(1.1)
Maoridiamesa harrisi	1550	3857	1298	624	292	1524.5
	(373.8)	(735.7)	(290.8)	(213.3)	(87.3)	(625.4)
Diamesinae sp. B	0	0	0	0	9	1.8
	-	-	-	-	(8.4)	(1.8)
Paucispinigera sp.	8	7	0	0	0	2.9
	(2.2)	(5.2)	-	-	-	(1.8)
Tanytarsus vespertinus	17	29	5	18	21	18.1
	(5.4)	(9.9)	(2.3)	(9.2)	(8.2)	(4.0)
?*Rheocricotopus* sp.	1419	2007	2027	415	89	1191.2
	(325.0)	(491.8)	(363.5)	(121.7)	(42.4)	(402.0)
Orthocladiinae sp. B	49	365	268	45	21	149.6
	(9.9)	(86.4)	(52.0)	(29.2)	(10.8)	(70.0)
Orthocladiinae sp. A	16	2	1	40	13	14.4
	(9.2)	(1.6)	(0.8)	(12.9)	(7.1)	(7.2)
Orthocladiinae sp. C	0	2	0	0	0	0.3
	-	(1.7)	-	-	-	(0.3)
Eukiefferiella claripennis	1023	1266	742	372	108	702.1
	(132.3)	(204.4)	(157.4)	(78.0)	(21.1)	(210.3)
Cricotopus aucklandensis	5	396	66	30	2	99.8
	(5.1)	(127.9)	(24.1)	(11.2)	(1.6)	(75.0)
Nothodixa sp.	0	0	0	2	0	0.5
	-	-	-	(1.9)	-	(0.5)
Empididae sp. A	28	23	13	6	3	14.7
	(10.6)	(6.2)	(5.6)	(2.6)	(2.3)	(4.7)
Ephydridae ?	0	6	2	0	0	1.6
	-	(5.1)	(1.7)	-	-	(1.2)
Limnophora sp. A	2	50	27	8	0	17.2
	(1.6)	(13.9)	(7.9)	(4.8)	-	(9.4)
Diptera indet.	0	1	0	0	0	0.2
	-	(0.8)	-	-	-	(0.2)
Hydrobiosis parumbripennis	1	14	11	11	8	8.9
	(0.8)	(3.7)	(5.3)	(4.9)	(5.1)	(2.2)

Hydrobiosis spatulata	11	2	6	0	1	3.9
	(5.3)	(1.7)	(2.4)	-	(0.8)	(2.1)
Hydrobiosis sp.	0	1	0	0	0	0.2
	-	(0.8)	-	-	-	(0.2)
Psilochorema bidens	0	0	2	0	0	0.3
	-	-	(1.7)	-	-	(0.3)
Psilochorema nemorale	0	0	0	4	2	1.1
	-	-	-	(4.2)	(1.6)	(0.8)
Costachorema xanthoptera	0	2	0	7	0	1.7
	-	(1.7)	-	(4.6)	-	(1.3)
Neurochorema confusum	2	2	1	2	0	1.4
	(1.9)	(1.6)	(0.8)	(1.0)	-	(0.5)
early instar Hydrobiosidae	79	115	88	53	43	75.6
	(16.7)	(26.1)	(17.2)	(23.1)	(26.7)	(12.7)
Oxyethira albiceps	5	14	9	10	1	7.6
	(3.4)	(5.6)	(4.1)	(4.8)	(0.8)	(2.2)
Paroxyethira eatoni	0	0	4	0	0	0.8
	-	-	(4.2)	-	-	(0.8)
Philorheithrus agilis	2	8	13	2	6	6.3
	(1.0)	(3.2)	(5.7)	(2.4)	(3.2)	(2.1)
Hudsonema aliena	2	0	9	18	0	5.8
	(1.6)	-	(3.8)	(12.0)	-	(3.6)
Zelolessica cheira	2	0	221	149	4	75.3
	(1.9)	-	(49.1)	(82.0)	(2.9)	(46.2)
Pycnocentria evecta	0	2	77	0	16	19.2
	-	(2.4)	(34.0)	-	(6.9)	(14.8)
Pycnocentrodes sp.	59	121	202	462	112	191.3
	(18.0)	(62.1)	(36.9)	(200.7)	(32.5)	(71.5)
Beraeoptera roria	179	26	171	165	188	145.8
	(44.6)	(8.5)	(30.7)	(36.1)	(41.6)	(30.2)
Olinga feredayi	37	33	216	140	57	96.8
	(15.7)	(12.8)	(55.8)	(32.4)	(11.9)	(35.6)
Oribatei sp. A	13	13	14	5	12	11.4
	(3.8)	(6.7)	(3.8)	(2.3)	(5.7)	(1.6)
Hydrachenellae sp. A	85	166	137	250	33	134.2
	(43.2)	(90.8)	(45.3)	(91.4)	(16.2)	(36.8)
Notoaturinae sp. A	57	65	235	80	81	103.5
	(12.5)	(14.1)	(44.8)	(16.3)	(19.4)	(33.2)
Hydrachenellae sp. C	8	0	0	0	0	1.6
	(4.9)	-	-	-	-	(1.6)
Notoaturinae sp. D	0	0	2	0	0	0.3
	-	-	(1.0)	-	-	(0.3)
Hygrobatidae sp. B	0	0	0	1	0	0.2
	-	-	-	(0.8)	-	(0.2)
parasitic mite	0	0	0	0	3	0.6
	-	-	-	-	(2.3)	(0.6)
pupae	75	112	124	16	57	76.8
	(19.5)	(24.9)	(30.1)	(5.5)	(11.9)	(19.4)
Number of species	49	54	57	51	44	51.0 (2.2)
Total number of individuals	5907	9383	8083	3736	1939	5809.6 (1364.3)

SLIP SPRING

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Hydridae sp. A	10	11	11	21	5	11.5
	(4.8)	(5.3)	(4.9)	(10.0)	(4.3)	(2.7)
Hydridae sp. B	0	3	1	0	0	0.7
	-	(2.7)	(0.9)	-	-	(0.5)
Neppia montana	98	120	135	332	192	175.5
	(28.6)	(44.5)	(28.8)	(102.5)	(58.6)	(42.0)
Spathula sp.	2	65	25	78	44	42.9
	(1.4)	(24.2)	(10.9)	(36.5)	(14.4)	(13.6)
Rhabdocoela	5	10	3	35	10	12.6
	(2.8)	(9.2)	(2.3)	(18.8)	(4.7)	(5.7)
Nematoda sp. A	2	4	8	6	15	6.9
	(1.3)	(2.3)	(3.6)	(1.7)	(8.3)	(2.3)
Potamopyrgus antipodarum	795	1751	906	1704	875	1206.4
	(196.5)	(362.5)	(358.9)	(580.1)	(391.5)	(213.7)
Slavina sp.	36	1079	460	203	156	386.7
	(16.2)	(432.6)	(156.1)	(69.9)	(91.1)	(186.3)
Eiseniella sp.	0	0	0	1	0	0.2
	-	-	-	(0.9)	-	(0.2)
Tubificidae sp.	0	0	0	0	1	0.2
	-	-	-	-	(0.9)	(0.2)
Lumbriculus variegatus	0	1	0	0	0	0.2
	-	(0.9)	-	-	-	(0.2)
Oligocheata sp.	0	219	99	17	4	67.8
	-	(66.1)	(33.5)	(8.2)	(2.9)	(41.8)
Tardigrada sp. A	0	17	9	75	53	30.8
	-	(15.3)	(8.2)	(63.0)	(25.8)	(14.3)
Chydoridae sp.	1	2	0	0	1	0.6
	(0.7)	(1.1)	-	-	(0.7)	(0.3)
Ostracoda sp. A	2	4	2	3	0	2.2
	(1.3)	(1.7)	(1.8)	(2.8)	-	(0.6)
Harpacticoid Copepoda	141	476	158	877	329	396.2
	(77.0)	(249.6)	(127.3)	(636.5)	(181.0)	(135.0)
Paraleptamphopus subterraneus	239	312	73	101	53	155.7
	(81.7)	(141.6)	(29.1)	(33.5)	(34.5)	(50.9)
Collembola	2	7	0	11	4	4.9
	(1.3)	(4.5)	-	(4.3)	(2.1)	(1.9)
Deleatidium sp. (*myzobranchia*-group)	35	183	301	162	162	168.4
	(13.5)	(67.3)	(90.4)	(33.6)	(42.0)	(42.2)
Stenoperla maclellani	0	1	3	6	1	1.9
	-	(0.7)	(1.1)	(2.0)	(0.7)	(1.0)
Zelandobius furcillatus	0	0	5	1	0	1.1
	-	-	(2.8)	(0.7)	-	(0.9)
Zelandobius pilosus	4	4	5	1	3	3.5
	(2.7)	(2.8)	(2.9)	(0.9)	(2.0)	(0.7)
Staphylinidae	0	4	0	0	0	0.8
	-	(4.2)	-	-	-	(0.8)
Scirtidae sp. B	2	6	0	19	9	7.1
	(1.3)	(3.6)	-	(14.6)	(5.2)	(3.2)
Aphrophila neozelandica	0	5	1	3	0	1.8
	-	(4.5)	(0.9)	(1.8)	-	(1.0)
Limonia nigrescens	1	1	9	13	4	5.5
	(0.9)	(0.9)	(3.6)	(7.1)	(2.4)	(2.4)

Austrosimulium laticorne	2	129	40	2	94	53.4
	(2.1)	(54.6)	(18.8)	(2.1)	(44.8)	(25.3)
Macropelopiini sp.	0	0	0	1	0	0.2
	-	-	-	(0.9)	-	(0.2)
Parochlus sp. A	120	53	2	27	5	41.4
	(46.2)	(19.3)	(1.1)	(27.3)	(3.0)	(21.7)
Maoridiamesa harrisi	2532	8007	4284	5514	8772	5821.9
	(608.1)	(1557.7)	(973.4)	(1381.1)	(3045.9)	(1156.8)
Lobodiamesa campbelli	0	4	0	0	0	0.8
	-	(4.2)	-	-	-	(0.8)
Diamesinae sp. A	0	0	0	1	0	0.1
	-	-	-	(0.7)	-	(0.1)
Paucispinigera sp.	1	5	0	5	1	2.4
	(0.9)	(2.8)	-	(2.9)	(1.3)	(1.1)
Tanytarsus vespertinus	0	1	11	6	6	4.7
	-	(0.9)	(6.2)	(3.3)	(2.8)	(1.9)
?*Rheocricotopus* sp.	166	1994	1529	1847	212	1149.5
	(53.4)	(662.7)	(387.2)	(554.1)	(46.4)	(399.4)
Orthocladiinae sp. B	3	34	8	64	44	30.7
	(1.3)	(13.3)	(3.7)	(37.3)	(16.2)	(11.3)
Orthocladiinae sp. A	4	0	18	105	58	37.0
	(2.5)	-	(7.3)	(47.0)	(34.5)	(19.8)
Orthocladiinae sp. C	0	47	0	0	0	9.5
	-	(14.3)	-	-	-	(9.5)
Eukiefferiella claripennis	110	158	1526	157	840	558.4
	(26.2)	(52.2)	(1486.6)	(56.1)	(317.7)	(277.4)
Eukiefferiella sp. B	0	1	1	0	3	0.9
	-	(0.7)	(0.7)	-	(2.5)	(0.6)
Cricotopus aucklandensis	0	104	16	7	0	25.4
	-	(30.6)	(7.4)	(2.7)	-	(19.9)
Nothodixa sp.	1	0	0	0	0	0.2
	(0.9)	-	-	-	-	(0.2)
Empididae sp. A	0	7	12	2	8	5.8
	-	(3.5)	(5.6)	(1.9)	(2.5)	(2.1)
Empididae sp. B	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Ephydridae ?	0	57	0	0	1	11.5
	-	(53.5)	-	-	(0.9)	(11.3)
Limnophora sp. A	7	23	8	4	18	12.0
	(5.5)	(6.6)	(4.4)	(1.7)	(6.2)	(3.7)
Limnophora sp. B	0	9	0	0	2	2.1
	-	(4.6)	-	-	(1.1)	(1.7)
Aoteapsyche colonica	0	1	0	0	0	0.2
	-	(0.9)	-	-	-	(0.2)
Hydrobiosis parumbripennis	4	18	13	11	3	9.8
	(2.5)	(7.0)	(5.3)	(4.3)	(1.1)	(2.8)
Psilochorema bidens	0	0	0	1	0	0.2
	-	-	-	(0.9)	-	(0.2)
Psilochorema nemorale	0	0	0	1	0	0.2
	-	-	-	(0.9)	-	(0.2)
Psilochorema macroharpax	0	1	0	0	0	0.2
	-	(0.9)	-	-	-	(0.2)
Psilochorema tautoru	0	1	0	0	0	0.2
	-	(0.9)	-	-	-	(0.2)
Costachorema xanthoptera	0	0	0	2	0	0.4
	-	-	-	(2.1)	-	(0.4)

early instar Hydrobiosidae	10	90	68	78	73	63.8
	(3.4)	(44.8)	(17.6)	(31.9)	(20.8)	(14.0)
Oxyethira albiceps	7	59	6	20	0	18.4
	(5.1)	(31.5)	(3.1)	(8.7)	-	(10.6)
Philorheithrus agilis	0	17	3	8	7	7.1
	-	(5.2)	(2.0)	(4.7)	(3.6)	(2.9)
Hudsonema aliena	1	4	8	4	1	3.4
	(0.7)	(2.7)	(6.5)	(4.0)	(0.9)	(1.3)
Zelolessica cheira	5	1	52	21	32	22.0
	(2.8)	(0.7)	(28.3)	(8.4)	(16.0)	(9.4)
Pycnocentria evecta	0	1	0	0	0	0.2
	-	(0.9)	-	-	-	(0.2)
Pycnocentrodes sp.	0	0	4	2	23	5.8
	-	-	(2.4)	(1.6)	(19.0)	(4.4)
Beraeoptera roria	0	0	2	0	4	1.1
	-	-	(1.1)	-	(3.6)	(0.7)
Olinga feredayi	1	1	12	0	2	3.1
	(0.9)	(0.9)	(5.8)	-	(2.0)	(2.2)
Oribatei sp. A	24	45	2	6	3	15.9
	(16.2)	(30.2)	(1.1)	(4.8)	(1.4)	(8.2)
Hydrachenellae sp. A	91	250	166	241	379	225.3
	(40.4)	(88.7)	(47.7)	(84.9)	(143.2)	(48.0)
Hydrachenellae sp. B	0	0	0	0	2	0.4
	-	-	-	-	(1.1)	(0.4)
Notoaturinae sp. A	73	167	243	159	136	155.6
	(33.5)	(49.5)	(119.9)	(41.0)	(51.6)	(27.3)
Notoaturinae sp. B	0	0	0	0	15	3.0
	-	-	-	-	(7.9)	(3.0)
Hydrachenellae sp. C	10	2	50	10	0	14.4
	(7.1)	(1.1)	(26.0)	(10.6)	-	(9.2)
Notoaturinae sp. C	0	0	0	0	2	0.4
	-	-	-	-	(2.1)	(0.4)
Thyasidae sp.	0	8	0	0	0	1.6
	-	(8.2)	-	-	-	(1.6)
Piona uncata exigua (nymph)	0	0	0	0	4	0.8
	-	-	-	-	(3.0)	(0.8)
Hygrobatidae sp. B	0	0	0	0	1	0.2
	-	-	-	-	(0.9)	(0.2)
parasitic mite	0	0	0	1	25	5.2
	-	-	-	(0.7)	(13.4)	(5.0)
pupae	14	44	20	13	214	61.0
	(5.6)	(13.0)	(7.5)	(6.6)	(166.5)	(38.6)
Number of species	37	55	44	50	50	47.2 (3.1)
Total number of individuals	4655	16047	10454	12327	13524	11401.4 (1915.1)

CORA LYNN STREAM

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Hydridae sp. A	4	1	19	0	0	5.0
	(2.9)	(0.6)	(11.2)	(0.5)	-	(3.7)
Neppia montana	47	29	31	33	75	43.1
	(16.9)	(11.5)	(15.3)	(11.6)	(32.2)	(8.6)
Spathula sp.	0	0	0	1	0	0.3
	-	-	-	(1.4)	-	(0.3)
Rhabdocoela	5	3	0	0	1	1.8
	(2.0)	(1.8)	-	-	(1.4)	(0.9)
Nematoda sp. A	22	16	27	3	8	15.3
	(7.6)	(8.1)	(13.2)	(1.5)	(4.2)	(4.4)
Gordius sp.	0	0	0.4	0	0	0.1
	-	-	(0.5)	-	-	(0.1)
Potamopyrgus antipodarum	1809	2246	2709	375	26	1433.0
	(386.8)	(571.3)	(742.7)	(84.5)	(9.9)	(525.8)
Gyraulus corinna	0	0	0	0.4	0	0.1
	-	-	-	(0.5)	-	(0.1)
Slavina sp.	99	98	449	42	0	137.7
	(22.9)	(34.9)	(194.3)	(16.9)	-	(80.0)
Eiseniella sp.	0	0	0	0	20	4.0
	-	-	-	-	(5.4)	(4.0)
Tubificidae sp.	0	0	0	5	0	1.2
	-	(0.5)	-	(5.5)	-	(1.1)
Lumbriculus variegatus	0	0	5	0	3	1.6
	-	-	(5.5)	-	(1.7)	(1.1)
Oligocheata sp.	0	0	5	0	0	1.1
	-	-	(5.5)	-	-	(1.1)
Chydoridae sp.	0	0	15	2	0	3.3
	-	-	(4.5)	(1.4)	-	(2.8)
Ostracoda sp. A	64	46	45	21	2	35.6
	(23.6)	(25.7)	(23.0)	(8.7)	(1.4)	(10.9)
Harpacticoid Copepoda	12	30	30	4	0	15.1
	(4.6)	(13.9)	(16.6)	(1.8)	(0.5)	(6.3)
Cyclopoid Copepoda	0	0	6	0	0	1.2
	-	-	(2.1)	-	-	(1.2)
Collembola	12	7	7	7	25	11.4
	(6.2)	(2.0)	(5.6)	(2.4)	(7.6)	(3.4)
Nesameletus sp.	4	2	7	7	1	4.2
	(2.8)	(1.4)	(5.6)	(5.5)	(1.4)	(1.2)
Deleatidium sp. (*myzobranchia*-group)	236	136	182	132	68	150.7
	(50.0)	(30.7)	(40.8)	(20.5)	(12.9)	(28.0)
Stenoperla maclellani	8	1	12	5	0	5.3
	(5.8)	(1.4)	(6.8)	(5.5)	-	(2.2)
Austroperla cyrene	6	0	4	2	0	2.3
	(2.4)	-	(1.9)	(1.5)	-	(1.1)
Zelandoperla decorata	0	3	8	0	0	2.2
	-	(2.8)	(5.4)	(0.5)	-	(1.5)
Zelandoperla agnetis	0	0	0.4	0	0	0.1
	-	-	(0.5)	-	-	(0.1)
Zelandobius furcillatus	2	9	37	9	0	11.4
	(1.8)	(6.2)	(16.0)	(4.0)	-	(6.6)
Zelandobius unicolor	0	0	19	0	0	3.7
	-	-	(12.4)	-	-	(3.7)

Zelandobius pilosus	6	13	53	0	0	14.4
	(5.5)	(7.0)	(21.9)	-	-	(10.0)
Zelandobius sp.	23	10	38	18	3	18.4
	(7.1)	(4.3)	(14.3)	(8.9)	(1.6)	(6.0)
Spaniocerca zelandica	4	11	15	3	2	7.0
	(1.8)	(5.4)	(7.6)	(1.7)	(1.4)	(2.7)
Hydrophilidae larvae indet.	1	0	0	0	0	0.3
	(1.4)	-	-	-	-	(0.3)
Orchymontia spinipennis	4	7	2	0	0	2.6
	(2.8)	(5.7)	(1.4)	-	-	(1.3)
Homalaena spatulata	0	0	6	0	0	1.3
	-	-	(5.5)	(0.5)	-	(1.2)
Scirtidae sp. B	0	0	2	0	0	0.5
	(0.5)	(0.5)	(1.4)	-	-	(0.3)
Scirtidae sp. C	0	0	0	3	0	0.5
	-	-	-	(1.7)	-	(0.5)
Elmidae larvae sp. A	25	12	9	4	0	10.1
	(8.5)	(6.2)	(6.8)	(1.9)	-	(4.3)
Neocurupira chiltoni	0	0	0.4	0	0	0.1
	-	-	(0.5)	-	-	(0.1)
Aphrophila neozelandica	5	0	0	0	0	1.0
	(2.9)	-	-	-	-	(1.0)
Limonia nigrescens	0	0	0.4	0	0	0.1
	-	-	(0.5)	-	-	(0.1)
?Molophilus sp.	0	0	0	0	1	0.3
	-	-	-	-	(1.4)	(0.3)
Ceratopogonidae	0.4	0	0	0	0	0.1
	(0.5)	-	-	-	-	(0.1)
Austrosimulium laticorne	6	2	4	0	0	2.5
	(2.9)	(1.6)	(4.1)	(0.5)	-	(1.1)
Macropelopiini sp.	10	3	38	0	0	10.2
	(2.6)	(1.5)	(38.2)	-	(0.5)	(7.1)
Parochlus sp. A	20	17	10	0	0	9.4
	(8.3)	(6.6)	(6.9)	-	-	(4.2)
Parochlus sp. B	0	1	0	1	5	1.7
	(0.5)	(1.4)	-	(1.4)	(5.5)	(0.9)
Maoridiamesa harrisi	185	368	37	19	33	128.4
	(62.7)	(148.6)	(22.5)	(8.4)	(12.8)	(67.0)
Paucispinigera sp.	0	1	3	0	0	0.8
	-	(1.4)	(1.7)	-	-	(0.5)
Tanytarsus vespertinus	4	1	0	4	0	1.8
	(1.8)	(1.4)	(0.5)	(1.8)	-	(0.8)
?Rheocricotopus sp.	386	192	68	43	15	140.7
	(94.5)	(52.8)	(26.9)	(11.1)	(11.3)	(68.3)
Limnophyes sp.	0	0	0	1	1	0.4
	-	-	-	(0.9)	(1.4)	(0.3)
Orthocladiinae sp. B	6	98	37	1	16	31.6
	(2.2)	(31.2)	(19.3)	(1.4)	(16.4)	(17.7)
Orthocladiinae sp. A	11	0	0	0	0	2.1
	(6.8)	-	-	-	-	(2.1)
Eukiefferiella claripennis	141	46	12	18	19	47.1
	(34.7)	(30.7)	(11.0)	(11.2)	(11.2)	(24.3)
Cricotopus aucklandensis	0	78	5	0	0	16.5
	-	(37.3)	(2.6)	-	-	(15.3)
Corynoneura scutellata	0	0	1	0	0	0.2
	-	-	(0.9)	-	-	(0.2)

Tanyderidae	5	0	0	0	0	1.1
	(5.5)	-	-	-	-	(1.1)
Nothodixa sp.	3	4	0	0	0	1.3
	(1.7)	(2.2)	-	-	-	(0.8)
Stratiomyidae	0	1	0	0	0	0.3
	-	(1.4)	-	-	-	(0.3)
Empididae sp. A	7	26	11	0	0	8.9
	(5.7)	(12.4)	(6.9)	(0.5)	-	(4.7)
Empididae sp. B	0	0	0	1	0	0.2
	-	-	-	(0.6)	-	(0.2)
Ephydridae ?	0	1	0	0	0	0.2
	-	(0.6)	-	-	-	(0.2)
Limnophora sp. A	1	2	0	0	0	0.7
	(0.6)	(1.5)	(0.5)	-	-	(0.4)
Diptera indet.	0	0	0	0	3	0.6
	-	-	-	-	(2.8)	(0.6)
Hydrobiosella stenocerca	0.4	0	0	0	0	0.1
	(0.5)	-	-	-	-	(0.1)
Aoteapsyche rarurarv	9	1	84	0	2	19.3
	(4.6)	(1.4)	(84.1)	-	(1.4)	(16.2)
Hydrobiosis parumbripennis	0	1	0	0	0	0.3
	-	(1.4)	-	-	-	(0.3)
Hydrobiosis sp.	0	0.4	0	0	0	0.1
	-	(0.5)	-	-	-	(0.1)
Psilochorema bidens	0	0	0.4	0	0	0.1
	-	-	(0.5)	-	-	(0.1)
Psilochorema nemorale	1	0	7	0	0	1.6
	(0.6)	-	(5.7)	-	-	(1.4)
Psilochorema tautoru	0	0	0.4	0	0	0.1
	-	-	(0.5)	-	-	(0.1)
Edpercivalia maxima	0	0	0.4	0	0	0.1
	-	-	(0.5)	-	-	(0.1)
Hydrochorema tenuicaudatum	0.4	0	0	0	0	0.1
	(0.5)	-	-	-	-	(0.1)
Costachorema callista	2	0	0	0	0	0.4
	(1.4)	-	-	-	-	(0.4)
Neurochorema confusum	0	0	11	0	0	2.2
	-	(0.5)	(10.9)	-	-	(2.1)
early instar Hydrobiosidae	38	9	22	14	1	16.8
	(21.7)	(3.9)	(13.2)	(6.3)	(1.4)	(6.3)
Oxyethira albiceps	10	8	29	0	0	9.5
	(5.9)	(5.7)	(12.0)	(0.5)	-	(5.2)
Paroxyethira eatoni	0	1	1	0	0	0.4
	-	(0.6)	(1.4)	-	-	(0.3)
Oeconesus similis ?	0	0	11	0	0	2.1
	-	-	(10.9)	-	-	(2.1)
Zelandopsyche ingens	0	2	0	0	0	0.4
	-	(1.4)	(0.5)	-	-	(0.3)
Philorheithrus agilis	18	8	25	0	0	10.4
	(11.7)	(5.8)	(16.1)	(0.5)	-	(5.0)
Zelolessica cheira	0	0	82	0	8	18.0
	-	-	(32.0)	(0.5)	(6.7)	(16.0)
Pycnocentria evecta	13	5	152	0	70	48.1
	(7.9)	(5.5)	(62.9)	-	(38.1)	(28.8)
Pycnocentrodes sp.	15	10	31	3	224	56.5
	(8.0)	(7.0)	(12.9)	(1.6)	(108.2)	(42.1)

Beraeoptera roria	95	98	53	18	3	53.4
	(35.4)	(36.4)	(42.6)	(6.1)	(1.8)	(19.3)
Olinga feredayi	65	21	107	13	0	41.1
	(24.1)	(8.3)	(63.7)	(5.8)	-	(19.7)
Oribatei sp. A	43	53	38	12	2	29.6
	(13.0)	(14.1)	(19.5)	(4.9)	(1.5)	(9.6)
Oribatei sp. B	0	0	0	2	0	0.4
	-	-	-	(1.4)	-	(0.4)
Hydrachenellae sp. A	197	210	227	37	5	135.3
	(151.9)	(99.5)	(101.9)	(18.5)	(5.5)	(47.1)
Notoaturinae sp. A	11	21	63	10	0	21.0
	(3.5)	(10.9)	(33.7)	(4.7)	-	(10.9)
Hydrachenellae sp. C	0	0.4	0	0	0	0.1
	-	(0.5)	-	-	-	(0.1)
Notoaturinae sp. D	0.4	0	0	0	0	0.1
	(0.5)	-	-	-	-	(0.1)
Notoaturinae sp. E	0	0	5	0	0	1.1
	-	-	(5.5)	-	-	(1.1)
parasitic mite	1	0	0	1	0	0.4
	(0.6)	-	-	(1.4)	-	(0.3)
pupae	29	11	8	3	0	10.1
	(10.4)	(4.1)	(6.6)	(1.6)	(0.5)	(5.0)
Number of species	54	54	64	45	30	49.4
						(5.7)
Total number of individuals	3752	3265	4015	727	405	2432.8
						(773.2)

MIDDLE BUSH STREAM

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Neppia montana	62	58	24	29	51	44.7
	(11.7)	(15.3)	(8.0)	(9.6)	(18.4)	(7.8)
Rhabdocoela	0	0	0	0	1	0.3
	-	-	-	-	(1.4)	(0.3)
Nematoda sp. A	70	75	41	21	0	41.2
	(12.9)	(19.7)	(12.3)	(6.5)	-	(14.2)
Potamopyrgus antipodarum	0	0	3	0	0	0.6
	-	-	(1.8)	-	-	(0.6)
Slavina sp.	237	10	0	44	7	59.5
	(41.7)	(3.5)	-	(13.8)	(4.2)	(45.0)
Eiseniella sp.	0	140	106	46	11	60.5
	-	(47.3)	(29.2)	(24.4)	(4.7)	(27.2)
Tubificidae sp.	0	0	5	5	2	2.3
	-	-	(2.7)	(2.3)	(1.6)	(1.1)
Lumbriculus variegatus	0	1	0	0	0	0.1
	-	(0.7)	-	-	-	(0.1)
Tardigrada sp. A	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Chydoridae sp.	5	0	0	0	0	1.0
	(2.9)	-	-	-	-	(1.0)
Ostracoda sp. A	266	89	306	111	18	157.9
	(83.4)	(29.8)	(141.0)	(26.5)	(6.7)	(54.9)
Ostracoda sp. C	0	0	1	0	0	0.3
	-	-	(1.4)	-	-	(0.3)
Harpacticoid Copepoda	12	0	1	3	0	3.1
	(4.0)	-	(0.7)	(2.8)	-	(2.2)
Collembola	38	18	2	7	18	16.6
	(6.6)	(7.0)	(0.9)	(2.9)	(6.6)	(6.2)
Microchorista philpotti	0	0	0	1	0	0.1
	-	-	-	(0.7)	-	(0.1)
Nesameletus sp.	30	10	11	17	8	15.0
	(10.8)	(4.0)	(4.7)	(5.2)	(4.1)	(3.9)
Deleatidium sp. (*myzobranchia*-group)	59	35	107	106	43	70.0
	(13.2)	(12.6)	(25.6)	(17.6)	(11.3)	(15.4)
Stenoperla maclellani	2	0	4	0	1	1.4
	(1.6)	-	(2.5)	-	(0.7)	(0.8)
Austroperla cyrene	1	0	0	0	0	0.3
	(1.4)	-	-	-	-	(0.3)
Acroperla spiniger	0	1	1	0	0	0.4
	-	(0.7)	(1.4)	-	-	(0.3)
Zelandobius furcillatus	12	0	2	2	0	3.3
	(7.4)	-	(1.4)	(1.4)	-	(2.3)
Zelandobius confusus	1	12	0	0	0	2.8
	(1.4)	(4.1)	-	-	-	(2.4)
Zelandobius unicolor	0	1	1	0	5	1.5
	-	(1.4)	(1.4)	-	(3.5)	(0.9)
Zelandobius pilosus	1	0	1	3	0	0.8
	(0.7)	-	(0.7)	(1.7)	-	(0.5)
Spaniocerca zelandica	127	55	80	39	11	62.6
	(26.5)	(21.5)	(33.6)	(14.8)	(7.1)	(19.7)
Cristaperla fimbria	5	0	3	1	3	2.6
	(3.2)	-	(2.7)	(1.4)	(3.4)	(0.8)

Hydrophilidae larvae indet.	0	0	0	0	1	0.1
	-	-	-	-	(0.7)	(0.1)
Staphylinidae	0	1	0	1	3	1.2
	-	(1.4)	-	(1.4)	(3.4)	(0.6)
Orchymontia spinipennis	8	13	1	5	4	6.1
	(3.2)	(4.7)	(0.7)	(2.3)	(2.0)	(2.1)
Homalaena spatulata	20	17	6	12	5	12.1
	(6.2)	(5.1)	(3.6)	(3.5)	(4.3)	(3.0)
Hydraenidae larvae sp. A	0	0	1	0	0	0.1
	-	-	(0.7)	-	-	(0.1)
Scirtidae sp. A	1	0	0	0	0	0.3
	(1.4)	-	-	-	-	(0.3)
Scirtidae sp. B	17	4	6	2	0	5.8
	(5.3)	(2.0)	(2.3)	(1.4)	-	(3.0)
Scirtidae sp. C	0	0	1	0	1	0.3
	-	-	(0.7)	-	(0.7)	(0.2)
Scirtidae sp. D	0	4	0	0	0	0.8
	-	(2.2)	-	-	-	(0.8)
Elmidae larvae sp. A	2	3	6	0	0	2.2
	(1.6)	(1.7)	(3.8)	-	-	(1.1)
Eriopterini sp.	0	1	0	0	0	0.1
	-	(0.7)	-	-	-	(0.1)
Limonia nigrescens	0	1	0	1	0	0.4
	-	(0.7)	-	(1.4)	-	(0.3)
?*Molophilus* sp.	1	0	0	0	0	0.3
	(1.4)	-	-	-	-	(0.3)
Ceratopogonidae	4	0	1	0	1	1.2
	(2.9)	-	(0.9)	-	(0.7)	(0.8)
Forcipomyiinae sp. A	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
Forcipomyiinae sp. B	1	0	0	0	0	0.3
	(1.4)	-	-	-	-	(0.3)
Austrosimulium albovelatum	4	14	5	8	8	7.8
	(2.9)	(5.5)	(2.9)	(4.2)	(4.3)	(1.7)
Thaumaleidae	0	3	0	0	0	0.6
	-	(2.8)	-	-	-	(0.6)
Macropelopiini sp.	79	19	31	7	9	28.9
	(24.6)	(5.5)	(14.6)	(2.3)	(4.2)	(13.1)
Maoridiamesa harrisi	0	1	0	0	0	0.3
	-	(1.4)	-	-	-	(0.3)
Paucispinigera sp.	234	113	137	49	1	106.9
	(44.1)	(43.4)	(48.9)	(13.8)	(1.4)	(39.8)
Polypedilum sp.	1	0	0	0	0	0.3
	(1.4)	-	-	-	-	(0.3)
Tanytarsus vespertinus	1	1	0	3	3	1.9
	(0.9)	(1.4)	-	(2.9)	(2.9)	(0.7)
Tanytarsus sp.	0	19	1	8	3	6.4
	-	(8.2)	(1.4)	(4.0)	(1.7)	(3.6)
?*Rheocricotopus* sp.	42	90	31	12	10	37.0
	(6.9)	(26.1)	(9.1)	(4.7)	(4.6)	(14.4)
Orthocladiinae sp. C	5	0	1	0	2	1.6
	(3.7)	-	(1.4)	-	(1.6)	(0.9)
Eukiefferiella claripennis	5	2	3	4	1	3.3
	(3.7)	(1.6)	(1.7)	(3.5)	(0.9)	(0.7)
Eukiefferiella sp. B	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)

Cricotopus aucklandensis	2	2	0	0	0	0.8
	(1.6)	(1.6)	-	-	-	(0.5)
Nothodixa sp.	6	8	7	3	0	4.7
	(2.0)	(3.9)	(2.8)	(1.7)	-	(1.4)
Empididae sp. A	0	0	0	6	0	1.2
	-	-	-	(3.6)	-	(1.2)
Empididae sp. B	33	32	23	6	8	20.4
	(8.9)	(9.6)	(8.4)	(3.2)	(3.0)	(5.8)
Empididae sp. C	0	0	0	0	1	0.3
	-	-	-	-	(1.4)	(0.3)
Limnophora sp. A	0	0	0	0	1	0.1
	-	-	-	-	(0.7)	(0.1)
Diptera indet.	0	0	1	1	0	0.3
	-	-	(0.7)	(0.7)	-	(0.2)
Osmylidae	1	0	0	0	0	0.3
	(1.4)	-	-	-	-	(0.3)
Hydrobiosella stenocerca	15	4	7	5	8	8.0
	(5.9)	(2.5)	(4.5)	(3.5)	(3.4)	(1.9)
Aoteapsyche colonica	0	2	0	0	0	0.4
	-	(1.6)	-	-	-	(0.4)
Aoteapsyche raruraru	0	0	1	0	0	0.1
	-	-	(0.7)	-	-	(0.1)
Hydrobiosis spatulata	1	0	0	0	0	0.1
	(0.7)	-	-	-	-	(0.1)
early instar Hydrobiosidae	8	37	17	12	1	15.1
	(4.1)	(10.2)	(7.4)	(3.8)	(1.4)	(6.1)
Zelandopsyche ingens	2	3	1	2	0	1.6
	(0.9)	(1.8)	(1.4)	(1.4)	-	(0.5)
Philorheithrus agilis	46	4	34	11	2	19.6
	(14.0)	(2.5)	(12.6)	(4.6)	(1.6)	(8.8)
Zelolessica cheira	0	0	1	0	0	0.3
	-	-	(1.4)	-	-	(0.3)
Pycnocentria sylvestris	0	0	0	0	1	0.3
	-	-	-	-	(1.4)	(0.3)
Pycnocentrodes sp.	0	1	0	0	0	0.3
	-	(1.4)	-	-	-	(0.3)
Olinga feredayi	10	10	10	1	0	5.9
	(4.1)	(3.9)	(6.8)	(0.7)	-	(2.3)
Oribatei sp. A	3	2	12	4	1	4.4
	(1.7)	(1.6)	(7.5)	(2.6)	(1.4)	(1.8)
Hydrachenellae sp. A	1	14	19	4	5	8.6
	(0.7)	(4.4)	(9.8)	(3.5)	(3.7)	(3.4)
Hydrachenellae sp. B	0	0	0	0	2	0.4
	-	-	-	-	(0.9)	(0.4)
Notoaturinae sp. A	8	79	70	20	8	37.0
	(3.3)	(21.5)	(24.9)	(8.6)	(3.4)	(15.6)
Hydrachenellae sp. C	0	2	6	1	0	1.9
	-	(1.6)	(3.8)	(1.4)	-	(1.1)
Notoaturinae sp. D	7	0	0	0	0	1.4
	(3.3)	-	-	-	-	(1.4)
Hygrobatidae sp. A	0	1	0	0	0	0.3
	-	(1.4)	-	-	-	(0.3)
Hydrachenellae sp. E	0	0	0	1	0	0.3
	-	-	-	(1.4)	-	(0.3)
parasitic mite	0	1	0	0	0	0.1
	-	(0.7)	-	-	-	(0.1)

pupae	4 (2.5)	3 (1.9)	1 (0.9)	1 (0.9)	0 -	2.1 (0.8)
Number of species	49	46	46	41	38	44.0 (2.0)
Total number of individuals	1338	931	1157	642	239	861.4 (194.3)

GRASMERE STREAM

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Hydridae sp. A	1	0	0	1	9	2.0
	(0.6)	-	-	(0.6)	(5.1)	(1.7)
Hydridae sp. B	6	3	0	0	0	1.9
	(4.4)	(1.2)	-	-	-	(1.3)
Neppia montana	7	3	0	0	0	2.0
	(4.9)	(2.3)	-	-	-	(1.5)
Rhabdocoela	0	2	0	0	4	1.2
	-	(2.2)	-	-	(2.9)	(0.8)
Nematoda sp. A	0	59	141	116	6	64.1
	-	(18.4)	(59.2)	(72.8)	(2.8)	(28.3)
Potamopyrgus antipodarum	89	75	99	49	6	63.7
	(29.2)	(28.5)	(41.2)	(20.5)	(2.7)	(16.8)
Physa sp.	0	18	2	0	0	4.0
	-	(13.3)	(2.2)	-	-	(3.5)
Lymnaea tomentosa	0	0	0	1	0	0.1
	-	-	-	(0.6)	-	(0.1)
Slavina sp.	71	0	0	14	5	17.8
	(21.2)	-	-	(9.6)	(2.8)	(13.4)
Eiseniella sp.	0	148	402	83	67	140.0
	-	(41.5)	(213.7)	(27.4)	(25.7)	(69.6)
Tubificidae sp.	1	1	0	0	17	3.8
	(0.8)	(0.6)	-	-	(12.4)	(3.4)
Lumbriculus variegatus	0	0	1	0	0	0.2
	-	-	(0.8)	-	-	(0.2)
Oligocheata sp.	0	3	0	0	1	0.7
	-	(2.3)	-	-	(0.6)	(0.5)
Tardigrada sp. A	0	19	6	1	0	5.2
	-	(15.8)	(4.6)	(1.3)	-	(3.6)
Chydoridae sp.	1	50	10	48	69	35.6
	(0.8)	(14.6)	(5.5)	(19.2)	(12.6)	(12.8)
Bosmina meridionalis	0	0	0	157	5	32.4
	-	-	-	(39.5)	(2.8)	(31.2)
Ostracoda sp. A	15	2	14	10	6	9.3
	(6.9)	(1.3)	(9.2)	(4.7)	(4.5)	(2.4)
Ostracoda sp. B	0	2	0	0	0	0.4
	-	(2.2)	-	-	-	(0.4)
Harpacticoid Copepoda	11	10	2	10	10	8.3
	(6.6)	(4.4)	(1.0)	(5.3)	(4.3)	(1.7)
Cyclopoid Copepoda	11	3	23	29	14	16.1
	(3.0)	(2.3)	(7.8)	(10.5)	(5.0)	(4.5)
Collembola	22	0	0	2	32	11.1
	(8.9)	-	-	(1.3)	(13.2)	(6.6)
Coloburiscus humeralis	19	70	97	96	8	57.9
	(10.3)	(18.7)	(23.6)	(39.7)	(3.5)	(19.0)
Nesameletus sp.	5	1	2	2	0	2.2
	(4.4)	(1.3)	(2.2)	(2.2)	-	(0.9)
Deleatidium sp. (*myzobranchia*-group)	334	81	0	236	180	166.2
	(58.1)	(18.5)	-	(54.4)	(51.1)	(58.4)
Deleatidium sp. (*lillii*-group)	0	0	227	0	0	45.4
	-	-	(53.9)	-	-	(45.4)
Zelandoperla decorata	4	0	0	0	0	0.8
	(4.2)	-	-	-	-	(0.8)

Zelandobius confusus	0	1	0	0	0	0.2
	-	(1.3)	-	-	-	(0.2)
Zelandobius unicolor	0	1	0	5	0	1.1
	-	(0.6)	-	(4.2)	-	(0.9)
Archichauliodes diversus	0	3	1	1	2	1.4
	-	(2.3)	(0.8)	(0.6)	(2.2)	(0.6)
Microvelia sp.	0	0	0	0	1	0.1
	-	-	-	-	(0.6)	(0.1)
Scirtidae sp. B	2	0	0	0	0	0.4
	(2.2)	-	-	-	-	(0.4)
Scirtidae sp. C	0	0	0	0	4	0.8
	-	-	-	-	(2.7)	(0.8)
Elmidae larvae sp. A	14	27	20	6	13	16.0
	(5.4)	(10.3)	(9.3)	(5.6)	(8.1)	(3.5)
Aphrophila neozelandica	26	414	34	42	32	109.8
	(11.2)	(74.3)	(9.6)	(13.0)	(10.6)	(76.2)
Ceratopogonidae	0	0	0	0	2	0.4
	-	-	-	-	(2.2)	(0.4)
Austrosimulium albovelatum	988	39	14	18	24	216.6
	(199.3)	(14.5)	(5.9)	(7.0)	(11.8)	(192.9)
Macropelopiini sp.	3	1	0	2	0	1.2
	(2.3)	(0.6)	-	(2.2)	-	(0.7)
Parochlus sp. A	10	1	0	0	0	2.0
	(5.5)	(0.6)	-	-	-	(1.9)
Parochlus sp. B	0	0	0	0	2	0.4
	-	-	-	-	(2.2)	(0.4)
Maoridiamesa harrisi	760	1753	1005	1419	162	1019.8
	(222.7)	(258.3)	(196.0)	(252.5)	(74.5)	(273.9)
Paucispinigera sp.	7	0	0	0	0	1.5
	(4.8)	-	-	-	-	(1.5)
Tanytarsus vespertinus	4	0	5	0	0	1.8
	(2.7)	-	(4.3)	-	-	(1.1)
?*Rheocricotopus* sp.	322	1945	244	155	62	545.8
	(110.6)	(396.6)	(68.4)	(53.5)	(17.9)	(352.6)
Orthocladiinae sp. B	0	0	0	23	1	4.8
	-	-	-	(9.7)	(0.6)	(4.6)
Orthocladiinae sp. A	0	2	0	0	0	0.4
	-	(2.2)	-	-	-	(0.4)
Eukiefferiella claripennis	283	1226	346	187	109	430.5
	(48.4)	(169.1)	(79.5)	(49.0)	(28.2)	(203.1)
Eukiefferiella sp. B	0	172	23	0	0	39.0
	-	(45.3)	(8.0)	-	-	(33.5)
Cricotopus aucklandensis	86	3948	185	82	4	860.9
	(21.7)	(811.2)	(66.9)	(25.0)	(2.5)	(772.3)
Nothodixa sp.	0	2	1	3	5	2.2
	-	(2.2)	(0.8)	(2.3)	(2.8)	(0.9)
Empididae sp. A	0	5	0	0	0	1.1
	-	(2.8)	-	-	-	(1.1)
Empididae sp. B	0	0	1	0	0	0.2
	-	-	(0.8)	-	-	(0.2)
Empididae sp. C	2	0	0	0	0	0.4
	(2.2)	-	-	-	-	(0.4)
Limnophora sp. A	0	7	0	0	0	1.3
	-	(3.2)	-	-	-	(1.3)
Limnophora sp. B	1	0	0	0	0	0.1
	(0.6)	-	-	-	-	(0.1)
Diptera indet.	0	0	0	2	0	0.4
	-	-	-	(2.2)	-	(0.4)

Polyplectropus puerilis	2	0	0	0	0	0.4
	(2.2)	-	-	-	-	(0.4)
Aoteapsyche colonica	119	1661	342	164	165	490.3
	(44.5)	(261.1)	(129.0)	(39.7)	(47.5)	(295.1)
Aoteapsyche raruraru	0	0	1	0	0	0.2
	-	-	(0.8)	-	-	(0.2)
Hydrobiosis parumbripennis	10	22	6	3	2	8.7
	(6.0)	(6.9)	(2.8)	(2.3)	(2.2)	(3.6)
Hydrobiosis spatulata	7	1	0	1	0	1.7
	(2.8)	(0.8)	-	(0.6)	-	(1.2)
Psilochorema nemorale	1	7	3	1	0	2.4
	(0.6)	(5.0)	(2.3)	(1.3)	-	(1.3)
Psilochorema macroharpax	0	0	1	0	0	0.2
	-	-	(0.8)	-	-	(0.2)
Psilochorema tautoru	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)
Costachorema brachyptera	0	0	0	0	2	0.4
	-	-	-	-	(2.2)	(0.4)
Neurochorema confusum	33	127	48	60	14	56.3
	(9.4)	(27.4)	(12.5)	(24.7)	(7.0)	(19.2)
early instar Hydrobiosidae	31	210	59	10	12	64.4
	(10.2)	(43.1)	(14.3)	(4.9)	(6.2)	(37.5)
Oxyethira albiceps	9	34	4	8	0	10.8
	(4.5)	(9.9)	(2.4)	(4.5)	-	(6.1)
Hudsonema aliena	0	3	0	0	0	0.7
	-	(2.5)	-	-	-	(0.7)
Hudsonema amabilis	3	10	4	1	1	3.9
	(2.5)	(7.8)	(4.3)	(1.3)	(0.6)	(1.7)
Zelolessica cheira	0	0	21	5	0	5.0
	-	-	(10.2)	(2.9)	-	(4.0)
Pycnocentria evecta	233	405	462	419	30	309.7
	(48.3)	(100.3)	(150.4)	(95.7)	(19.3)	(80.1)
Pycnocentrodes sp.	112	33	47	156	14	72.4
	(17.8)	(11.8)	(12.0)	(46.3)	(7.7)	(26.6)
Beraeoptera roria	3	5	12	43	3	13.1
	(2.3)	(2.6)	(6.1)	(13.9)	(2.5)	(7.7)
Olinga feredayi	85	58	77	54	41	62.7
	(32.0)	(14.3)	(27.7)	(27.5)	(31.6)	(8.0)
Conuxia gunni	0	0	0	2	0	0.4
	-	-	-	(2.2)	-	(0.4)
Oribatei sp. A	0	0	0	1	1	0.2
	-	-	-	(0.6)	(0.6)	(0.1)
Notoaturinae sp. A	2	10	5	0	2	3.8
	(1.6)	(4.9)	(2.8)	-	(1.9)	(1.7)
Hydrachenellae sp. C	0	0	0	9	0	1.8
	-	-	-	(4.7)	-	(1.8)
Notoaturinae sp. C	4	0	0	0	0	0.8
	(4.2)	-	-	-	-	(0.8)
Kritaturus sp.	0	0	0	0	1	0.2
	-	-	-	-	(0.8)	(0.2)
pupae	162	430	37	35	59	144.4
	(49.9)	(99.5)	(10.3)	(10.5)	(18.4)	(75.0)
Number of species	44	50	40	45	43	44.4 (1.6)
Total number of individuals	2825	9744	2621	3053	1084	3865.4 (1509.7)

LAKE GRASMERE

Taxon	Spring 1	Summer	Autumn	Winter	Spring 2	Average
Plumatella repens	0	4	0	0	0	0.9
	-	(4.4)	-	-	-	(0.9)
Hydridae sp. A	8	0	2	0	0	2.0
	(3.7)	-	(1.6)	-	-	(1.5)
Hydridae sp. B	0	49	8	0	0	11.4
	-	(8.9)	(4.6)	-	-	(9.5)
Neppia montana	0	0	0	2	0	0.4
	-	-	-	(2.1)	-	(0.4)
Cura pinguis	60	101	70	11	15	51.4
	(20.2)	(21.7)	(21.4)	(3.3)	(4.8)	(17.0)
Rhabdocoela	31	29	5	1	3	13.7
	(13.9)	(14.3)	(2.8)	(0.6)	(1.7)	(6.7)
Hirudinea sp.	0	3	1	0	0	0.8
	-	(1.8)	(0.8)	-	-	(0.6)
Nematoda sp. A	100	540	354	99	652	349.1
	(36.0)	(104.5)	(70.3)	(36.2)	(159.1)	(112.4)
Nematoda sp. B	0	0	0	1	0	0.2
	-	-	-	(0.8)	-	(0.2)
Potamopyrgus antipodarum	586	2136	1670	255	113	952.1
	(214.8)	(607.7)	(704.1)	(64.5)	(42.9)	(402.5)
Physa sp.	14	630	217	12	4	175.7
	(6.2)	(165.5)	(45.6)	(6.5)	(2.9)	(120.5)
Gyraulus kahuica	3	3	5	2	0	2.6
	(3.0)	(1.7)	(3.0)	(2.1)	-	(0.8)
Sphaerium novazelandiae	1	0	0	0	0	0.3
	(1.5)	-	-	-	-	(0.3)
Slavina sp.	792	2000	1378	2198	1908	1655.3
	(160.1)	(246.9)	(247.1)	(463.8)	(267.6)	(254.9)
Eiseniella sp.	0	0	0	0	107	21.3
	-	-	-	-	(23.6)	(21.3)
Tubificidae sp.	0	36	32	4	19	18.2
	-	(7.3)	(11.8)	(2.5)	(9.8)	(7.2)
Lumbriculus variegatus	0	4	0	2	2	1.6
	-	(2.2)	-	(1.6)	(1.6)	(0.8)
Oligocheata sp.	0	189	153	15	5	72.2
	-	(36.7)	(32.4)	(4.9)	(2.0)	(40.7)
Tardigrada sp. A	94	54	238	38	92	103.3
	(52.4)	(23.5)	(93.0)	(9.8)	(20.9)	(35.2)
Tardigrada sp. B	0	0	0	18	0	3.7
	-	-	-	(6.3)	-	(3.7)
Chydoridae sp.	4546	942	2430	497	395	1762.2
	(1547.5)	(139.4)	(348.0)	(116.9)	(83.9)	(785.4)
Bosmina meridionalis	0	0	190	0	19	41.8
	-	-	(40.0)	-	(7.7)	(37.1)
Ostracoda sp. A	19	29	55	5	20	25.4
	(9.5)	(11.0)	(15.7)	(2.9)	(6.5)	(8.3)
Harpacticoid Copepoda	36	66	86	50	148	77.4
	(15.6)	(17.7)	(23.2)	(29.5)	(35.0)	(19.6)
Cyclopoid Copepoda	20	15	83	24	4	29.4
	(8.9)	(5.8)	(23.9)	(10.2)	(2.7)	(13.9)
Collembola	1	2	3	0	2	1.7
	(1.5)	(2.1)	(2.2)	-	(1.6)	(0.5)

Deleatidium sp. (*myzobranchia*-group)	0	0	497	0	0	99.5
	-	-	(108.6)	-	-	(99.5)
Deleatidium sp. (*lillii*-group)	284	421	0	296	64	212.9
	(67.8)	(70.3)	-	(65.9)	(17.3)	(78.3)
Procordulia smithi	0	0	0	0	1	0.1
	-	-	-	-	(0.6)	(0.1)
Zygoptera sp.	0	0	1	0	0	0.1
	-	-	(0.6)	-	-	(0.1)
Stenoperla maclellani	18	39	14	4	7	16.3
	(4.5)	(12.0)	(10.8)	(2.5)	(4.3)	(6.1)
Stenoperla prasina	2	7	11	3	10	6.7
	(0.9)	(3.2)	(4.7)	(1.8)	(4.7)	(1.9)
Austroperla cyrene	65	35	11	8	1	24.2
	(43.0)	(14.8)	(5.5)	(3.4)	(0.8)	(11.8)
Zelandobius furcillatus	1	0	5	7	9	4.4
	(1.3)	-	(2.3)	(3.1)	(3.4)	(1.7)
Zelandobius pilosus	0	2	0	0	0	0.4
	-	(2.1)	-	-	-	(0.4)
Zelandobius sp.	7	0	0	0	0	1.4
	(3.2)	-	-	-	-	(1.4)
Sigara sp.	0	0	0	0	2	0.4
	-	-	-	-	(1.6)	(0.4)
Liodessus plicatus	1	0	0	0	0	0.1
	(0.6)	-	-	-	-	(0.1)
Elmidae larvae sp. A	1	5	4	0	0	2.1
	(1.5)	(3.3)	(2.5)	-	-	(1.1)
Limonia nigrescens	0	1	0	0	0	0.1
	-	(0.6)	-	-	-	(0.1)
Ceratopogonidae	0	0	0	0	1	0.3
	-	-	-	-	(1.5)	(0.3)
Austrosimulium albovelatum	0	1	0	0	0	0.3
	-	(1.5)	-	-	-	(0.3)
Macropelopiini sp.	8	7	7	3	1	5.2
	(4.1)	(3.4)	(6.1)	(2.0)	(0.6)	(1.4)
Parochlus sp. A	18	0	0	1	2	4.2
	(7.7)	-	-	(0.6)	(1.6)	(3.5)
Parochlus sp. B	1	0	0	0	0	0.1
	(0.6)	-	-	-	-	(0.1)
Maoridiamesa harrisi	121	2	10	11	5	29.7
	(32.9)	(1.6)	(3.6)	(3.4)	(2.7)	(22.8)
Paucispinigera sp.	2	3	3	0	0	1.6
	(1.3)	(1.9)	(1.8)	-	-	(0.7)
Tanytarsus vespertinus	11	3	11	23	26	14.5
	(4.6)	(1.7)	(4.4)	(6.4)	(7.6)	(4.2)
Tanytarsus sp.	0	0	0	0	11	2.1
	-	-	-	-	(5.7)	(2.1)
Chironomus sp.	0	0	1	0	0	0.1
	-	-	(0.6)	-	-	(0.1)
?*Cladopelma* sp.	0	0	0	0	2	0.4
	-	-	-	-	(2.1)	(0.4)
?*Rheocricotopus* sp.	61	22	132	94	10	63.6
	(23.0)	(4.6)	(29.4)	(33.5)	(4.7)	(22.7)
Limnophyes sp.	99	7	6	1	18	26.2
	(38.6)	(3.2)	(3.7)	(0.6)	(5.4)	(18.4)
Orthocladiinae sp. B	0	0	0	0	1	0.3
	-	-	-	-	(1.5)	(0.3)

Orthocladiinae sp. C	0	0	11	0	0	2.1
	-	-	(6.0)	-	-	(2.1)
Eukiefferiella claripennis	17	0	1	4	2	4.9
	(12.0)	-	(0.8)	(4.3)	(2.1)	(3.1)
Eukiefferiella sp. B	1421	844	728	1431	133	911.4
	(467.8)	(164.0)	(184.8)	(318.5)	(32.8)	(242.3)
Cricotopus aucklandensis	82	45	89	70	46	66.4
	(25.4)	(11.4)	(18.6)	(11.4)	(10.7)	(9.0)
Cricotopus sp.	5	0	6	11	0	4.2
	(2.7)	-	(2.9)	(4.8)	-	(2.0)
Stratiomyidae	1	0	0	0	0	0.2
	(0.8)	-	-	-	-	(0.2)
Empididae sp. B	0	2	0	0	0	0.4
	-	(2.1)	-	-	-	(0.4)
Ephydridae ?	2	0	0	0	0	0.4
	(1.3)	-	-	-	-	(0.4)
Neoscatella ?	1	0	0	0	0	0.1
	(0.6)	-	-	-	-	(0.1)
Ephydrella sp.	3	0	0	0	0	0.6
	(1.8)	-	-	-	-	(0.6)
Limnophora sp. A	1	0	0	0	1	0.4
	(1.5)	-	-	-	(0.6)	(0.3)
Polyplectropus puerilis	0	1	4	1	0	1.0
	-	(0.6)	(2.5)	(0.6)	-	(0.7)
Psilochorema bidens	0	0	0	1	0	0.1
	-	-	-	(0.6)	-	(0.1)
Neurochorema confusum	0	0	0	1	0	0.2
	-	-	-	(0.8)	-	(0.2)
Oxyethira albiceps	71	35	31	7	5	29.8
	(28.5)	(10.2)	(9.6)	(3.8)	(2.0)	(12.0)
Paroxyethira eatoni	1	0	1	0	1	0.6
	(0.6)	-	(1.3)	-	(1.5)	(0.3)
Paroxyethira hendersoni	1	1	12	0	0	2.7
	(1.5)	(0.6)	(3.5)	-	-	(2.2)
Oeconesus maori ?	0	0	0	0	1	0.1
	-	-	-	-	(0.6)	(0.1)
Hudsonema aliena	0	0	1	0	0	0.3
	-	-	(1.5)	-	-	(0.3)
Hudsonema amabilis	3	98	33	6	2	28.2
	(1.9)	(16.3)	(6.8)	(3.4)	(1.3)	(18.3)
Pycnocentrodes aureola	19	3168	225	193	47	730.4
	(6.6)	(679.4)	(48.4)	(61.8)	(16.4)	(610.8)
Oribatei sp. A	15	15	8	11	20	13.7
	(7.8)	(4.6)	(4.0)	(3.3)	(4.0)	(2.0)
Hydrachenellae sp. A	1	1	1	1	0	0.6
	(1.3)	(0.6)	(0.6)	(0.6)	-	(0.2)
Notoaturinae sp. A	4	4	2	1	1	2.5
	(2.5)	(2.6)	(2.1)	(0.8)	(0.8)	(0.6)
Hydrachenellae sp. C	0	0	0	0	1	0.3
	-	-	-	-	(1.5)	(0.3)
Hydrachenellae sp. D	0	5	0	0	0	1.0
	-	(2.6)	-	-	-	(1.0)
Piona uncata exigua (nymph)	0	6	16	0	0	4.4
	-	(4.3)	(4.9)	-	-	(3.2)
parasitic mite	0	0	0	10	0	1.9
	-	-	-	(7.2)	-	(1.9)

pupae	50 (20.9)	34 (6.6)	34 (8.9)	8 (3.7)	25 (8.4)	30.2 (6.7)
Number of species	48	46	49	43	46	46.4 (1.0)
Total number of individuals	9147	10993	8464	5481	3979	7612.8 (1270.0)

APPENDIX II

COMPUTER PROGRAMS

I have used computer programs written in Turbo BASIC throughout the course of my study. I have included examples of two such programs below, one I used to fit species-abundance models and the other which I used to model random colonisation and disturbance of communities in my basket experiment.

PROGRAM 1 - SPECIES-ABUNDANCE MODELS

```
'*************************************************************************************************
REM PROGRAM TO FIT LOG SERIES, TRUNCATED LOG NORMAL, BROKEN STICK, AND
GEOMETRIC SERIES DISTRIBUTIONS
'*************************************************************************************************

CLS
DEFDBL A - Z
DIM A(100), D(17), E(100), S$(100), S(17), L(17), C(17), P(100) B(17), V(6,100), Y(100), G(100)
DIM SList(100), F(100), Z(100), X(100)


'*************************************************************************************************
REM INPUT DATA
'*************************************************************************************************

U = 16
PRINT "WHAT SITE IS THIS": INPUT B$
A$ = "A:\TOTALS\" + B$ + ".COM"
PRINT "HOW MANY SPECIES ARE THERE": INPUT S
OPEN A$ FOR INPUT AS 1
FOR I = 1 TO S
        INPUT#1, S$(I)
        FOR J = 1 TO 6
                INPUT#1, V(J,I)
        NEXT J
        FOR J = 1 TO 5
                A(I) = A(I) + V(J,I)
        NEXT J
        IF A(I) > Z6 THEN Z6 = A(I)
        N = N + A(I)
NEXT I


REM SET UPPER LIMIT TO DISTRIBUTION

PRINT
PRINT USING "THE MAXIMUM DENSITY IS = ########";Z6
PRINT
PRINT "COMPARE WITH UPPER LIMITS FOR U = 16 OF 32768"
PRINT "                U = 15 OF 16384"
PRINT "                U = 14 OF 8192"
PRINT "                U = 13 OF 4096"
PRINT "                U = 12 OF 2048"
PRINT "                U = 11 OF 1024"
PRINT "                U = 10 OF 512"
PRINT "                U = 9  OF 256"
PRINT "                U = 8  OF 128"
PRINT "                U = 7  OF 64"
PRINT
```

```
PRINT "DO YOU WISH TO CHANGE U": INPUT P$
IF P$ = "y" OR P$ = "Y" THEN PRINT "WHAT IS THE NEW VALUE FOR U": INPUT U
PRINT
CLS
CLOSE 1


REM OBSERVED FREQUENCY DISTRIBUTION

FOR I = 1 TO S
        IF A(I) < = 1 THEN D(1) = D(1) + 1
        IF A(I) < = 2 AND A(I) > 1 THEN D(2) = D(2) + 1
        IF A(I) < = 4 AND A(I) > 2 THEN D(3) = D(3) + 1
        IF A(I) < = 8 AND A(I) > 4 THEN D(4) = D(4) + 1
        IF A(I) < = 16 AND A(I) > 8 THEN D(5) = D(5) + 1
        IF A(I) < = 32 AND A(I) > 16 THEN D(6) = D(6) + 1
        IF A(I) < = 64 AND A(I) > 32 THEN D(7) = D(7) + 1
        IF A(I) < = 128 AND A(I) > 64 THEN D(8) = D(8) + 1
        IF A(I) < = 256 AND A(I) > 128 THEN D(9) = D(9) + 1
        IF A(I) < = 512 AND A(I) > 256 THEN D(10) = D(10) + 1
        IF A(I) < = 1024 AND A(I) > 512 THEN D(11) = D(11) + 1
        IF A(I) < = 2048 AND A(I) > 1024 THEN D(12) = D(12) + 1
        IF A(I) < = 4096 AND A(I) > 2048 THEN D(13) = D(13) + 1
        IF A(I) < = 8192 AND A(I) > 4096 THEN D(14) = D(14) + 1
        IF A(I) < = 16384 AND A(I) > 8192 THEN D(15) = D(15) + 1
        IF A(I) < = 32768 AND A(I) > 16384 THEN D(16) = D(16) + 1
        IF A(I) > 32768 THEN PRINT: PRINT "****WARNING UPPER LIMIT EXCEEDED****"
NEXT I

GGO:
PRINT "WHAT DISTRIBUTION DO YOU WISH TO FIT"
PRINT "     1 = LOG SERIES"
PRINT "     2 = LOG NORMAL"
PRINT "     3 = BROKEN STICK "
PRINT "     4 = GEOMETRIC SERIES "
PRINT: INPUT FG
        IF FG = 1 THEN D$ = "LOG SERIES"
        IF FG = 2 THEN D$ = "LOG NORMAL"
        IF FG = 3 THEN D$ = "BROKEN STICK"
        IF FG = 4 THEN D$ = "GEOMETRIC SERIES"
CLS
        IF D$ = "LOG SERIES" THEN GOSUB LOGIT
        IF D$ = "LOG NORMAL" THEN GOSUB LOGNORM
        IF D$ = "BROKEN STICK" THEN GOSUB BROKEN
        IF D$ = "GEOMETRIC SERIES" THEN GOSUB GEOMETRIC
IF D$ = "LOG SERIES" OR D$ = "LOG NORMAL" OR D$ = "BROKEN STICK" THEN GOSUB GOODFIT
PRINT
PRINT "DO YOU WANT TO FIT ANOTHER MODEL": INPUT Z$
IF Z$ = "Y" OR Z$ = "y" THEN GOTO GGO
END


'*************************************************************************************************
REM LOG SERIES
'*************************************************************************************************

LOGIT:
B = 0
PRINT USING "WHAT IS THE START VALUE OF X GIVEN THAT N/S = #####.##";N/S
PRINT
PRINT "X IS ALWAYS 0.9 > X < 1.0"
PRINT "AND WHEN N/S > 20 X WILL BE GREATER THAN 0.99"
PRINT
PRINT: INPUT X
R = S/N

ITERATE:
        E = ((1 - X)/X)*( - 1*LOG(1 - X))
        IF ABS(R - E) > 0.001 AND E > R THEN X = X + 0.0001: GOTO ITERATE
        IF ABS(R - E) > 0.001 AND E < R THEN X = X - 0.0001: GOTO ITERATE
        IF ABS(R - E) > 0.00001 AND E > R THEN X = X + 0.000001: GOTO ITERATE
        IF ABS(R - E) > 0.00001 AND E < R THEN X = X - 0.000001: GOTO ITERATE
```

```
        IF ABS(R - E) > 0.000001 AND E > R THEN X = X + 0.0000001: GOTO ITERATE
        IF ABS(R - E) > 0.000001 AND E < R THEN X = X - 0.0000001: GOTO ITERATE
PRINT USING "ESITIMATE OF X = ##.#####";X
PRINT "REINPUT X": INPUT Y
A = N*(1 - Y)/Y
PRINT USING "ALPHA = ##.####";A


REM EXPECTED FREQUENCY FOR LOG SERIES

FOR J = 1 TO (U - 1)
        IF J = 1 THEN C = 1: C1 = 1
        IF J = 2 THEN C = 2: C1 = 2
        IF J = 3 THEN C = 3: C1 = 4
        IF J = 4 THEN C = 5: C1 = 8
        IF J = 5 THEN C = 9: C1 = 16
        IF J = 6 THEN C = 17: C1 = 32
        IF J = 7 THEN C = 33: C1 = 64
        IF J = 8 THEN C = 65: C1 = 128
        IF J = 9 THEN C = 129: C1 = 256
        IF J = 10 THEN C = 257: C1 = 512
        IF J = 11 THEN C = 513: C1 = 1024
        IF J = 12 THEN C = 1025: C1 = 2048
        IF J = 13 THEN C = 2049: C1 = 4096
        IF J = 14 THEN C = 4097: C1 = 8192
        IF J = 15 THEN C = 8193: C1 = 16384

        FOR I = C TO C1
                S(J) = S(J) + (A*(Y^I)/I)
        NEXT I
        B = B + (INT(S(J)*100))
NEXT J
S(U) = S - (B/100)

FOR J = 1 TO U
        E(J) = S(J)
        S(J) = 0
NEXT J
RETURN


'*****************************************************************************************************
REM LOGNORMAL DISTRIBUTION
'*****************************************************************************************************

LOGNORM:
V = 0: T = 0
X =  - 0.30103
FOR I = 1 TO S
        P(I) = LOG10(A(I))
        T = T + P(I)
NEXT I
M = T/S
FOR I = 1 TO S
        V = V + ((P(I) - M)^2)
NEXT I
V = V/(S - 1)
G = V/((M - X)^2)
PRINT USING "WHAT IS THE AUXILIARY ESTIMATION FUNCTION FOR G = ##.###";G: INPUT G
A = M - G*(M - X)
B = V + G*((M - X)^2)
Z = (X - A)/(SQR(B))

O = 1/SQR(2.*3.1415926536)
Q = 1/(1 + 0.2316419*(ABS(Z)))
H = Q*(0.319381530 + Q*(-0.356553782 + Q*(1.781477937 + Q*(-1.821255978 + Q*1.330274429))))
P = O*(EXP( - (ABS(Z))^2/2))*H
P = 0.5 - P
IF Z < 0 THEN P = 0.5 - P
IF Z > 0 THEN P = 0.5 + P
E = S/(1 - P)
```

```
REM EXPECTED FREQUENCY FOR LOG NORMAL

FOR J = 1 TO U
        IF J = 1 THEN L = (LOG10(0.5) - A)/(SQR(B))
        IF J = 2 THEN L = (LOG10(1) - A)/(SQR(B))
        IF J = 3 THEN L = (LOG10(2) - A)/(SQR(B))
        IF J = 4 THEN L = (LOG10(4) - A)/(SQR(B))
        IF J = 5 THEN L = (LOG10(8) - A)/(SQR(B))
        IF J = 6 THEN L = (LOG10(16) - A)/(SQR(B))
        IF J = 7 THEN L = (LOG10(32) - A)/(SQR(B))
        IF J = 8 THEN L = (LOG10(64) - A)/(SQR(B))
        IF J = 9 THEN L = (LOG10(128) - A)/(SQR(B))
        IF J = 10 THEN L = (LOG10(256) - A)/(SQR(B))
        IF J = 11 THEN L = (LOG10(512) - A)/(SQR(B))
        IF J = 12 THEN L = (LOG10(1024) - A)/(SQR(B))
        IF J = 13 THEN L = (LOG10(2048) - A)/(SQR(B))
        IF J = 14 THEN L = (LOG10(4096) - A)/(SQR(B))
        IF J = 15 THEN L = (LOG10(8192) - A)/(SQR(B))
        IF J = 16 THEN L = (LOG10(16384) - A)/(SQR(B))


        REM CALCULATE AREA UNDER THE NORMAL CURVE

        Q = 1/(1 + 0.2316419*(ABS(L)))
        H = Q*(0.319381530 + Q*( - 0.356553782 + Q*(1.781477937 + Q*( - 1.821255978 + Q*1.330274429))))
        P = O*(EXP( - (ABS(L))^2/2))*H
        P = 0.5 - P
        IF L < 0 THEN P = 0.5 - P
        IF L > 0 THEN P = 0.5 + P
        L(J) = E*P
NEXT J

L(U + 1) = E
FOR J = 1 TO (U + 1)
        C(J) = L(J) - L(J - 1)
NEXT J
FOR J = 1 TO U
        E(J) = C(J + 1)
NEXT J

PRINT USING "VEIL   ###.##";L(1)
RETURN


'*************************************************************************************************
REM BROKEN STICK MODEL
'*************************************************************************************************

BROKEN:
B = 0
FOR J = 1 TO (U - 1)
        IF J = 1 THEN C = 1: C1 = 1
        IF J = 2 THEN C = 2: C1 = 2
        IF J = 3 THEN C = 3: C1 = 4
        IF J = 4 THEN C = 5: C1 = 8
        IF J = 5 THEN C = 9: C1 = 16
        IF J = 6 THEN C = 17: C1 = 32
        IF J = 7 THEN C = 33: C1 = 64
        IF J = 8 THEN C = 65: C1 = 128
        IF J = 9 THEN C = 129: C1 = 256
        IF J = 10 THEN C = 257: C1 = 512
        IF J = 11 THEN C = 513: C1 = 1024
        IF J = 12 THEN C = 1025: C1 = 2048
        IF J = 13 THEN C = 2049: C1 = 4096
        IF J = 14 THEN C = 4097: C1 = 8192
        IF J = 15 THEN C = 8193: C1 = 16384

        FOR I = C TO C1
                B(J) = B(J) + (S*(S - 1)/N)*((1 - I/N)^(S - 2))
        NEXT I
        B = B + (INT(B(J)*100))
NEXT J
```

```
B(U) = S - (B/100)

FOR J = 1 TO U
        E(J) = B(J)
        B(J) = 0
NEXT J
RETURN


'*************************************************************************************************
REM GEOMETRIC SERIES
'*************************************************************************************************

GEOMETRIC:
R = A(1): B = 0
FOR I = 1 TO S
        IF A(I) < R THEN R = A(I)
NEXT I
R = R/N: R = R*1000
PRINT "INPUT A STARTING VALUE FOR K. E.G. K = 0.42 ?": INPUT K

IITERATE:
        E = (K/(1 - K))*((1 - K)^S)/(1 - (1 - K)^S): P1 = P1 + 1
        IF P1 > 10000 AND P1 < 10020 THEN PRINT USING "##.##########";E*1000,R,K
        IF P1 > 10020 THEN END
        E = E*1000
        IF ABS(R - E) > 0.001 AND E > R THEN K = K + 0.0001: GOTO IITERATE
        IF ABS(R - E) > 0.001 AND E < R THEN K = K - 0.0001: GOTO IITERATE
        IF ABS(R - E) > 0.00001 AND E > R THEN K = K + 0.000001: GOTO IITERATE
        IF ABS(R - E) > 0.00001 AND E < R THEN K = K - 0.000001: GOTO IITERATE
        IF ABS(R - E) > 0.000001 AND E > R THEN K = K + 0.0000001: GOTO IITERATE
        IF ABS(R - E) > 0.000001 AND E < R THEN K = K - 0.0000001: GOTO IITERATE
PRINT USING "ESITIMATE OF K = ##.#####";K
PRINT "REINPUT K": INPUT K
A = (1 - (1 - K)^S)^(-1)
PRINT USING "C = ##.######";A
PRINT


REM EXPECTED FREQUENCY FOR GEOMETRIC SERIES

FOR I = 1 TO S
        E(I) = N*A*K*(1 - K)^(I - 1)
NEXT I
FOR I = 1 TO S
        SList(I) = A(I)
NEXT I

CALL QuickSort(1,S)

K = 1: I = S
        FOR C = 1 TO S
        F(K) = SList(I)
        I = S - K: K = K + 1
NEXT C


'*************************************************************************************************
REM GOODNESS OF FIT FOR DISTRIBUTIONAL DATA
'*************************************************************************************************

G = 0: V = 0: W = 0
FOR J = S TO 1 STEP - 1
        IF E(J + 1) > 1 AND E(J) < 1 THEN Q$ = "*****WARNING *****": W = S - W: GOTO SKIP
        IF E(J) < 1 THEN E(J - 1) = E(J) + E(J - 1): F(J - 1) = F(J - 1) + F(J): W = W + 1
NEXT J
W = S - W

GOTO SKIP

CCLEAR:
FOR J = 1 TO S
```

```
        F(J) = 0
        E(J) = 0
NEXT J
RETURN
END

DEF FNPartition(Left,Right)
        LOCAL Indx,Jndx,Value,Temp
        Value = SList(Right)
        Indx = Left - 1
        Jndx = Right
        DO
                DO
                Indx = Indx + 1
                LOOP UNTIL SList(Indx) > = Value
                DO
                Jndx = Jndx - 1
                LOOP UNTIL SList(Jndx) < = Value
                Temp = SList(Indx)
                SList(Indx) = SList(Jndx)
                SList(Jndx) = Temp
        LOOP UNTIL Jndx < = Indx
        SList(Jndx) = SList(Indx)
        SList(Indx) = SList(Right)
        SList(Right) = Temp
        FnPartition = Indx
END DEF

'QuickSort Recursive Procedure
SUB QuickSort(Left,Right)
        LOCAL Indx
        IF Left < = Right THEN
                Indx = FNPartition(Left,Right)
                Call QuickSort(Left,Indx - 1)
                Call QuickSort(Indx + 1,Right)
        END IF
END SUB


'*****************************************************************************************************
REM GOODNESS OF FIT
'*****************************************************************************************************

GOODFIT:
G = 0: V = 0: W = 0

FOR J = 1 TO U
        F(J) = D(J)
NEXT J

IF E(1) < 1 THEN PRINT "**** WARNING THERE IS REVERSE TRUNCTAION ****": W = U: GOTO SKIP
FOR J = U TO 1 STEP  - 1
        IF E(J + 1) > 1 AND E(J) < 1 THEN PRINT "****WARNING  *****": W = U - W: GOTO SKIP
        IF E(J) < 1 THEN E(J - 1) = E(J) + E(J - 1): F(J - 1) = F(J - 1) + F(J): W = W + 1
NEXT J
W = U

SKIP:
PRINT "    CLASS ","    OBSERVED","    EXPECTED","    CHI - SQUARE"
FOR J = 1 TO W
        Z(J) = ((F(J) - E(J))^2)/E(J)
NEXT J
FOR J = 1 TO W
        PRINT USING "  #########.##    ";J,F(J),E(J),Z(J)
        V = V + E(J)
        G = G + Z(J)
NEXT J
PRINT "DO YOU WANT A PRINT OUT OF THIS": INPUT Y$
IF Y$ = "Y" OR Y$ = "y" THEN GOSUB PPRINT
PRINT
PRINT USING "EXPECTED TOTAL = ########.##";V
PRINT USING "CHI SQUARE = ########.####";G
```

```
IF D$ = "LOG NORMAL" THEN PRINT USING "DEGREES OF FREEDOM = ####";W - 3
IF D$ < > "LOG NORMAL" THEN PRINT USING "DEGREES OF FREEDOM = ####";W - 1
PRINT
PRINT USING "THE TOTAL NUMBER OF COLLECTED INDIVIDUALS = #######";N
PRINT USING "THE NUMBER OF COLLECTED SPECIES = ###";S
IF D$ = "GEOMETRIC SERIES" THEN GOTO CCLEAR
RETURN

PPRINT:
LPRINT D$
LPRINT "    CLASS ","    OBSERVED","    EXPECTED","    CHI - SQUARE"
FOR J = 1 TO W
        LPRINT USING "  #########.##    ";J,F(J),E(J),Z(J)
NEXT J
RETURN

'*****************************************************************************************************
REM END OF LISTING
'*****************************************************************************************************
```

PROGRAM 2 - RANDOM COLONISATION AND DISTURBANCE

```
'*************************************************************************************************
REM PROGRAM TO MODEL COLONISATION PROCESSES FOLLOWING DISTURBANCES
'*************************************************************************************************

CLS
DEFINT C
DIM B(3,100), E(3,120), T(100), P(100), M(3), S(3), R1(3), R2(3)

PRINT "WHAT SITE IS BEING EXAMINED": INPUT A$
PRINT "HOW MANY SPECIES": INPUT N
PRINT "HOW MANY RUNS": INPUT M
T = 0


REM INPUT SPECIES POOL

SPECIES:
        B$ = "C:\TEMP\" + A$ + "SPEC.POL"
        OPEN B$ FOR INPUT AS 1
        FOR Z = 1 TO N
                INPUT#1, P(Z)
        NEXT Z
        CLOSE 1

T1 = TIMER
        FOR Z = 1 TO N
                T = T + P(Z)
                T(Z) = T
        NEXT Z


REM INPUT BASKET TOTALS
FOR I = 1 TO 12
        PRINT "INPUT THE NUMBER OF ANIMALS IN BASKET",I
        INPUT M(I)
NEXT I

RANDOMIZE TIMER

PRINT "     ONE - THREE         THREE - NINE          ONE - NINE"

FOR K = 1 TO M
PRINT USING "RUN ##     ";K,


'*************************************************************************************************
REM SIMULATE RANDOM COLONISATION
'*************************************************************************************************

DIM A(12,100), D(12,100), M1(12)

FOR J = 1 TO 12
C = 0: C2 = 0
        IF J = 1 OR J = 2 OR J = 3 OR J = 4 THEN
                Z = 9
                ELSEIF J = 5 OR J = 6 OR J = 7 OR J = 8 THEN
                Z = 3
                ELSE
                Z = 1
        END IF

        IF J = 1 THEN
        C1 = M1(1)
                ELSEIF J = 2 THEN: C1 = M1(2)
                ELSEIF J = 3 THEN: C1 = M1(3)
                ELSEIF J = 4 THEN: C1 = M1(4)
                ELSEIF J = 5 THEN: C1 = M1(5)
                ELSEIF J = 6 THEN: C1 = M1(6)
                ELSEIF J = 7 THEN: C1 = M1(7)
```

```
            ELSEIF J = 8 THEN: C1 = M1(8)
            ELSEIF J = 9 THEN: C1 = M1(9)
            ELSEIF J = 10 THEN: C1 = M1(10)
            ELSEIF J = 11 THEN: C1 = M1(11)
            ELSE
            C1 = M1(12)
      END IF

COMMUNITY:
      C = C + 1
      R = RND * T(N)
      IF R > 0 AND R < = T(1) THEN
      I = 1
            ELSEIF R > T(1) AND R < = T(2) THEN: I = 2
            ELSEIF R > T(2) AND R < = T(3) THEN: I = 3
            ELSEIF R > T(3) AND R < = T(4) THEN: I = 4
            ELSEIF R > T(4) AND R < = T(5) THEN: I = 5
            ELSEIF R > T(5) AND R < = T(6) THEN: I = 6
            ELSEIF R > T(6) AND R < = T(7) THEN: I = 7
            ELSEIF R > T(7) AND R < = T(8) THEN: I = 8
            ELSEIF R > T(8) AND R < = T(9) THEN: I = 9
            ELSEIF R > T(9) AND R < = T(10) THEN: I = 10

            ELSEIF R > T(10) AND R < = T(11) THEN: I = 11
            ELSEIF R > T(11) AND R < = T(12) THEN: I = 12
            ELSEIF R > T(12) AND R < = T(13) THEN: I = 13
            ELSEIF R > T(13) AND R < = T(14) THEN: I = 14
            ELSEIF R > T(14) AND R < = T(15) THEN: I = 15
            ELSEIF R > T(15) AND R < = T(16) THEN: I = 16
            ELSEIF R > T(16) AND R < = T(17) THEN: I = 17
            ELSEIF R > T(17) AND R < = T(18) THEN: I = 18
            ELSEIF R > T(18) AND R < = T(19) THEN: I = 19
            ELSEIF R > T(19) AND R < = T(20) THEN: I = 20

            ELSEIF R > T(20) AND R < = T(21) THEN: I = 21
            ELSEIF R > T(21) AND R < = T(22) THEN: I = 22
            ELSEIF R > T(22) AND R < = T(23) THEN: I = 23
            ELSEIF R > T(23) AND R < = T(24) THEN: I = 24
            ELSEIF R > T(24) AND R < = T(25) THEN: I = 25
            ELSEIF R > T(25) AND R < = T(26) THEN: I = 26
            ELSEIF R > T(26) AND R < = T(27) THEN: I = 27
            ELSEIF R > T(27) AND R < = T(28) THEN: I = 28
            ELSEIF R > T(28) AND R < = T(29) THEN: I = 29
            ELSEIF R > T(29) AND R < = T(30) THEN: I = 30

            ELSEIF R > T(30) AND R < = T(31) THEN: I = 31
            ELSEIF R > T(31) AND R < = T(32) THEN: I = 32
            ELSEIF R > T(32) AND R < = T(33) THEN: I = 33
            ELSEIF R > T(33) AND R < = T(34) THEN: I = 34
            ELSEIF R > T(34) AND R < = T(35) THEN: I = 35
            ELSEIF R > T(35) AND R < = T(36) THEN: I = 36
            ELSEIF R > T(36) AND R < = T(37) THEN: I = 37
            ELSEIF R > T(37) AND R < = T(38) THEN: I = 38
            ELSEIF R > T(38) AND R < = T(39) THEN: I = 39
            ELSEIF R > T(39) AND R < = T(40) THEN: I = 40

            ELSEIF R > T(40) AND R < = T(41) THEN: I = 41
            ELSEIF R > T(41) AND R < = T(42) THEN: I = 42
            ELSEIF R > T(42) AND R < = T(43) THEN: I = 43
            ELSEIF R > T(43) AND R < = T(44) THEN: I = 44
            ELSEIF R > T(44) AND R < = T(45) THEN: I = 45
            ELSEIF R > T(45) AND R < = T(46) THEN: I = 46
            ELSEIF R > T(46) AND R < = T(47) THEN: I = 47
            ELSEIF R > T(47) AND R < = T(48) THEN: I = 48
            ELSEIF R > T(48) AND R < = T(49) THEN: I = 49
            ELSEIF R > T(49) AND R < = T(50) THEN: I = 50

            ELSEIF R > T(50) AND R < = T(51) THEN: I = 51
            ELSEIF R > T(51) AND R < = T(52) THEN: I = 52
            ELSEIF R > T(52) AND R < = T(53) THEN: I = 53
            ELSEIF R > T(53) AND R < = T(54) THEN: I = 54
            ELSEIF R > T(54) AND R < = T(55) THEN: I = 55
```

```
            ELSEIF R > T(55) AND R < = T(56) THEN: I = 56
            ELSEIF R > T(56) AND R < = T(57) THEN: I = 57
            ELSEIF R > T(57) AND R < = T(58) THEN: I = 58
            ELSEIF R > T(58) AND R < = T(59) THEN: I = 59
            ELSEIF R > T(59) AND R < = T(60) THEN: I = 60

            ELSEIF R > T(60) AND R < = T(61) THEN: I = 61
            ELSEIF R > T(61) AND R < = T(62) THEN: I = 62
            ELSEIF R > T(62) AND R < = T(63) THEN: I = 63
            ELSEIF R > T(63) AND R < = T(64) THEN: I = 64
            ELSEIF R > T(64) AND R < = T(65) THEN: I = 65
            ELSEIF R > T(65) AND R < = T(66) THEN: I = 66
            ELSEIF R > T(66) AND R < = T(67) THEN: I = 67
            ELSEIF R > T(67) AND R < = T(68) THEN: I = 68
            ELSEIF R > T(68) AND R < = T(69) THEN: I = 69
            ELSEIF R > T(69) AND R < = T(70) THEN: I = 70

            ELSEIF R > T(70) AND R < = T(71) THEN: I = 71
            ELSEIF R > T(71) AND R < = T(72) THEN: I = 72
            ELSEIF R > T(72) AND R < = T(73) THEN: I = 73
            ELSEIF R > T(73) AND R < = T(74) THEN: I = 74
            ELSEIF R > T(74) AND R < = T(75) THEN: I = 75
            ELSEIF R > T(75) AND R < = T(76) THEN: I = 76
            ELSEIF R > T(76) AND R < = T(77) THEN: I = 77
            ELSEIF R > T(77) AND R < = T(78) THEN: I = 78
            ELSEIF R > T(78) AND R < = T(79) THEN: I = 79
            ELSEIF R > T(79) AND R < = T(80) THEN: I = 80
            ELSE
            I = 0
        END IF


A(J,I) = A(J,I) + 1
IF C2 = 0 THEN C3 = C1 ELSE C3 = C1 - A
IF C < C3 THEN GOTO COMMUNITY
A = 0

'*************************************************************************************************
REM SIMULATE RANDOM REMOVAL BY DISTURBANCE
'*************************************************************************************************

DISTURB:
        C2 = C2 + 1
        IF C2 = Z THEN GOTO NNEXT
                FOR I = 1 TO N
                        IF A(J,I) = 0 THEN GOTO SKIP
                                FOR Y = 1 TO A(J,I)
                                D = RND
                                IF D > 0.7393 THEN D(J,I) = D(J,I) + 1
                                NEXT Y
                SKIP:
                NEXT I
        FOR I = 1 TO N
                A = A + D(J,I)
                A(J,I) = D(J,I)
        NEXT I

        C = 0
        ERASE D
        GOTO COMMUNITY

NNEXT:
NEXT J

'*************************************************************************************************
REM CALCULATE MEANS AND EUCLIDEAN DISTANCES
'*************************************************************************************************

AVERAGE:
        B1 = 0: B2 = 0: B3 = 0
        FOR I = 1 TO N
                B(1,I) = (A(1,I) + A(2,I) + A(3,I) + A(4,I))/4
```

```
            B1 = B1 + B(1,I)
            B(2,I) = (A(5,I) + A(6,I) + A(7,I) + A(8,I))/4
            B2 = B2 + B(2,I)
            B(3,I) = (A(9,I) + A(10,I) + A(11,I) + A(12,I))/4
            B3 = B3 + B(3,I)
        NEXT I
        PRINT B1,B2,B3

EUCLID:
        FOR I = 1 TO N
            E(1,K) = E(1,K) + (((B(2,I)/B2) - (B(1,I)/B1))^2)
            E(2,K) = E(2,K) + (((B(3,I)/B3) - (B(2,I)/B2))^2)
            E(3,K) = E(3,K) + (((B(3,I)/B3) - (B(1,I)/B1))^2)
        NEXT I

FOR W = 1 TO 3
        E(W,K) = SQR(E(W,K))
        M(W) = M(W) + E(W,K)
NEXT W
PRINT USING "##.######   ##.######   ##.######";E(1,K);E(2,K);E(3,K)

ERASE A
NEXT K

REM RANGE
FOR W = 1 TO 3
        FOR K = 1 TO M
            IF K = 1 THEN R1(W) = E(W,K)
            IF E(W,K) < R1(W) THEN R1(W) = E(W,K)
            IF E(W,K) > R2(W) THEN R2(W) = E(W,K)
        NEXT K
NEXT W

REM AVERAGE
FOR W = 1 TO 3
        M(W) = M(W)/M
        FOR K = 1 TO M
            S(W) = S(W) + ((E(W,K) - M(W))^2)
        NEXT K
        S(W) = SQR(S(W)/(M - 1))
NEXT W

T2 = TIMER

'*************************************************************************************************
REM PRINT RESULTS
'*************************************************************************************************

PRINT
PRINT "                    ONE - THREE   THREE - NINE   ONE - NINE"
PRINT
PRINT USING "MEAN EUCLID MEASURE       = ##.#####   ##.#####    ##.#####";M(1);M(2);M(3)
PRINT USING "STANDARD DEVIATION OF EUCLID = ##.##### ##.##### ##.##### ";S(1);S(2);S(3)
PRINT
PRINT USING "MINIMUM VALUE           = ##.#####   ##.#####    ##.#####";R1(1);R1(2);R1(3)
PRINT USING "MAXIMUM VALUE           = ##.#####   ##.#####    ##.#####";R2(1);R2(2);R2(3)
PRINT
IF T2 > T1 THEN T3 = T2 - T1
IF T2 < T1 THEN T3 = (86400 - T2) + T1
PRINT USING "TIME FOR EXECUTION  = ######.## HRS";T3/60/60

C$ = "C:\TEMP\" + A$ + "EUCLID.DAT"
OPEN C$ FOR OUTPUT AS 1
FOR K = 1 TO M
        PRINT#1, USING "##.######   ##.######   ##.######";E(1,K);E(2,K);E(3,K)
NEXT K
CLOSE 1
END

'*************************************************************************************************
REM END OF LISTING
'*************************************************************************************************
```

APPENDIX III

COMMUNITY STRUCTURE ALONG A MOUNTAIN SPRING-BROOK AND THE IMPACT OF CATTLE GRAZING

INTRODUCTION

When I started my doctoral research in April, 1987 I originally planned to investigate the factors affecting macroinvertebrate community structure at four sites on the Porter River. The two headwater sites had weed beds of *Myriophyllum* sp. and *Callitriche stagnalis* and appeared to represent relatively stable environments, whereas the furthermost downstream site had neither weed beds nor any noticeable epilithic periphyton and appeared to be a relatively unstable habitat. The remaining site seemed to be intermediate in stability between these two extremes. Thus, although the size of the stream did not increase significantly, environmental stability appeared to decline progressively in a relatively short distance (4 km) as one moved downstream. I was planning to examine how this apparent change in stability affected community structure along the stream, however, just prior to my second sampling date grazing cattle completely removed the weed beds from both "stable" sites, thoroughly disturbing the surrounding substrate in the process. As the two stable sites could no longer be considered stable, the original study was abandoned. I did, however, discover a rather interesting change in the composition of the benthic invertebrate communities as one moved downstream, that appeared to be mimicked in the associated weed bed faunas. This appendix contains the results of the single sampling and observations on the subsequent faunal recovery in the weed beds below Slip Spring.

STUDY SITES

The locations of the study sites are shown in Fig. 1. The first three sites were on a tributary of the Porter River, and the fourth was on a second tributary, a similar sized stream, that appeared to differ only in stability. Physicochemical variables measured at each of the sites on 30 May 1987 are recorded in Table 1.

MATERIALS AND METHODS

Five Surber samples (0.02 m^2, mesh = 250 μm) were collected from each of the

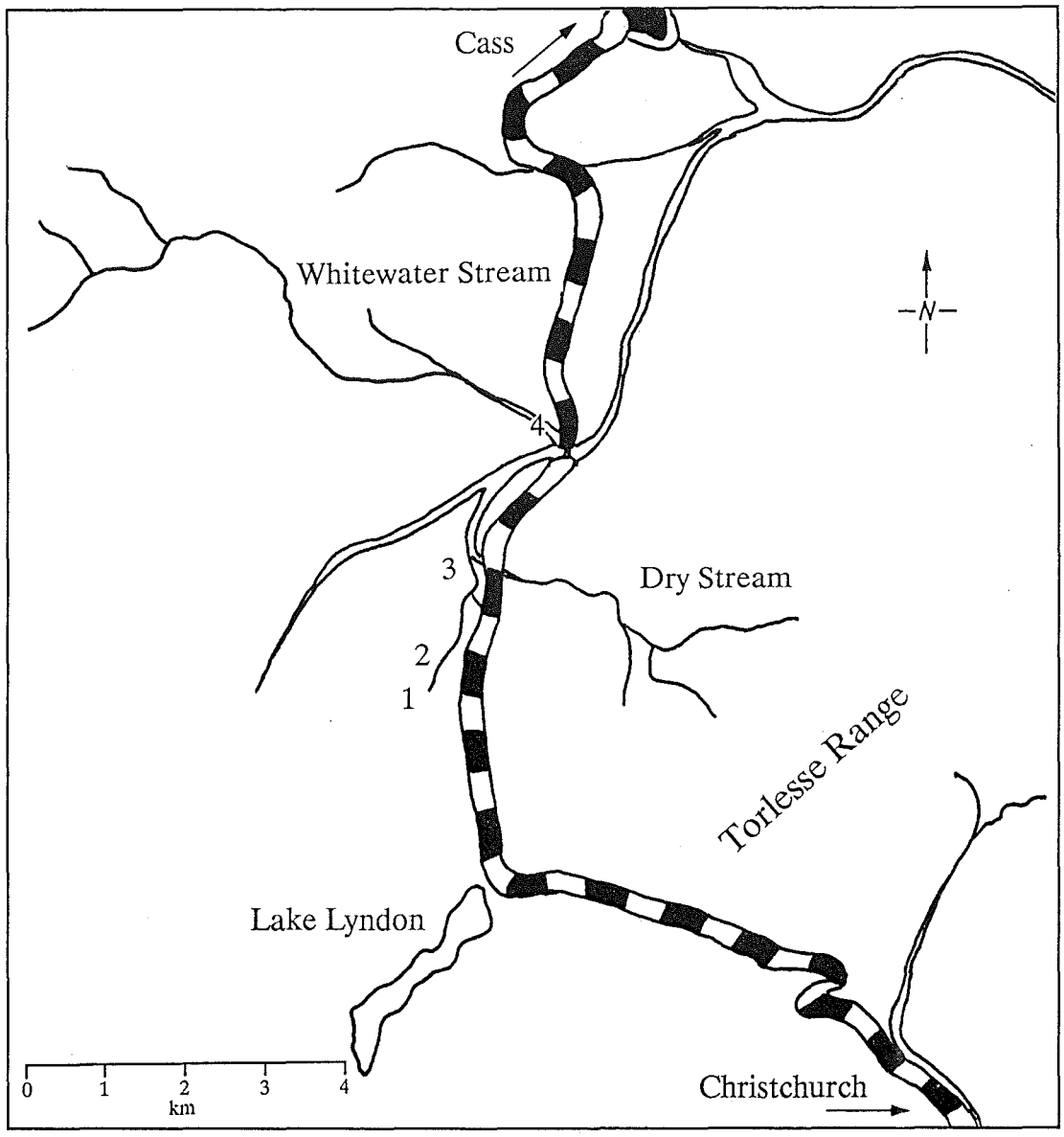


Figure 1. Map showing locations of the study sites.

Table 1. Current velocity, depth, spot temperature and pH recorded at each of the study sites on 30 May 1987. Depth was measured at the centre of the stream channel and current velocity at the same point 10 cm from the stream bed with a Pygmy Gurley current meter.

Site	Temperature °C	Depth cm	Current velocity cm s^{-1}	pH
Site 1	8.8	19 (16-24)	38	6.8
Site 2	8.9	18 (14-20)	60	7.2
Site 3	8.7	21 (20-21)	70	7.7
Site 4	7.8	15 (14-17)	81	7.6

sites on 30 May 1987. Samples at the two head water sites were taken so as to avoid the weed beds, which were sampled separately. This was achieved with a 0.02 m^2 quadrat and attached 250 μm mesh bag. Samples were frozen and returned to the laboratory for sorting. This was carried out as described in the main text (Chapter 4).

Samples at the disturbed Slip Spring weed beds were collected in a similar manner on 25 July, 4 August, 16 August and 9 September 1987. All samples were preserved in 10% formalin prior to sorting.

RESULTS

Numbers of taxa and total numbers of animals collected at each site are plotted in Figs 2 and 3, respectively. Both showed significant differences between sites ($F = 9.94, df = 1,16, P < 0.05$ and $F = 23.15, df = 1,16, P < 0.05$ for number of taxa and total numbers, respectively) and decreased downstream as stability declined. As only one seasonal sample was obtained no firm conclusions can be drawn from the data, however, three of the sites (sites 1, 3 and 4) were incorporated in my subsequent research program in which the same trend was found (Figs. 4 and 5).

The relative abundances of the five most abundant taxa at each site are shown in Fig. 6, and it is apparent that marked differences occurred between sites. Site 1 was strongly dominated by *Maoridiamesa harrisi* and *Potamopyrgus antipodarum*,

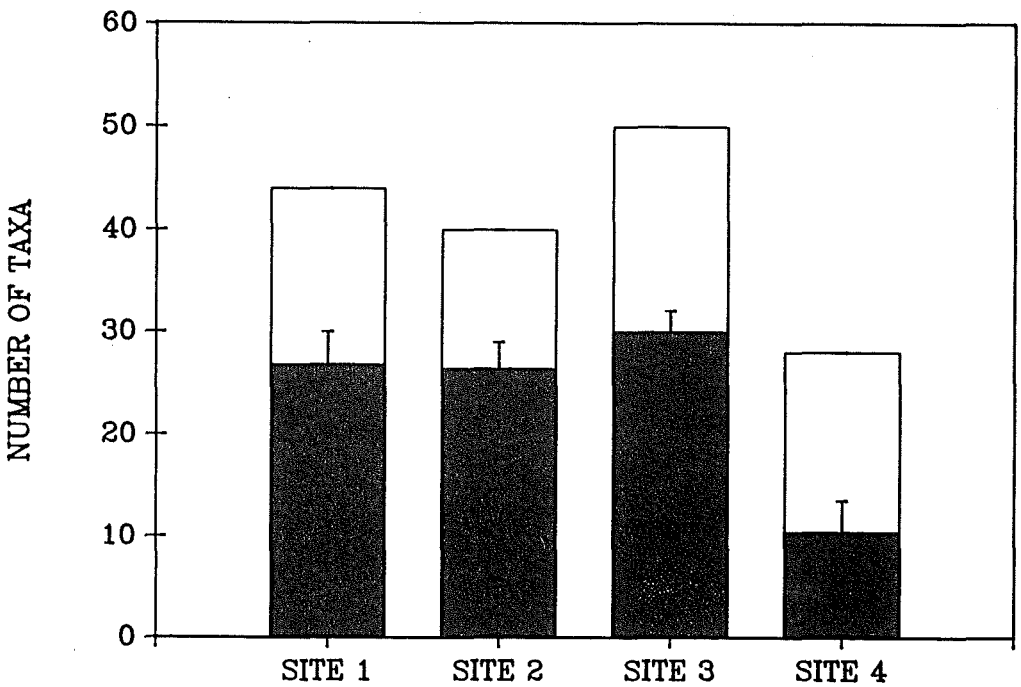


Figure 2. Mean number (± 1 SE) (solid bars) and total number of taxa (open bars) in 0.02 m^2 Surber samples, collected from the study sites on 30 May 1987.

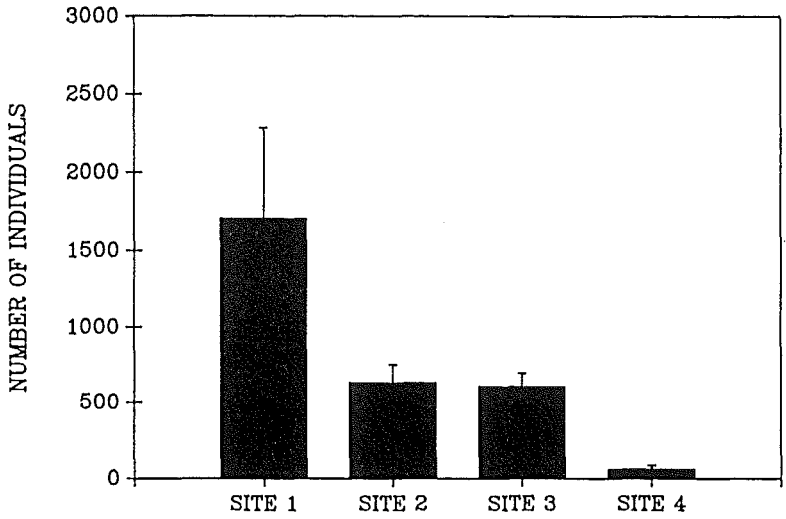


Figure 3. Mean number (± 1 SE) of invertebrates taken in 0.02 m^2 Surber samples, collected from the study sites on 30 May 1987.

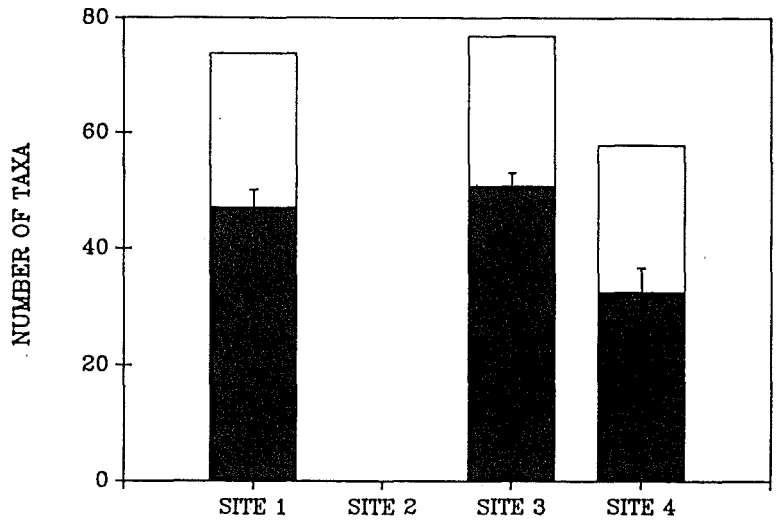


Figure 4. Mean number (± 1 SE) (solid bars) and total number of taxa (open bars) collected from three of the study sites in samples comprising 15 stones taken during the course of the main study (October 1987 - October 1988).

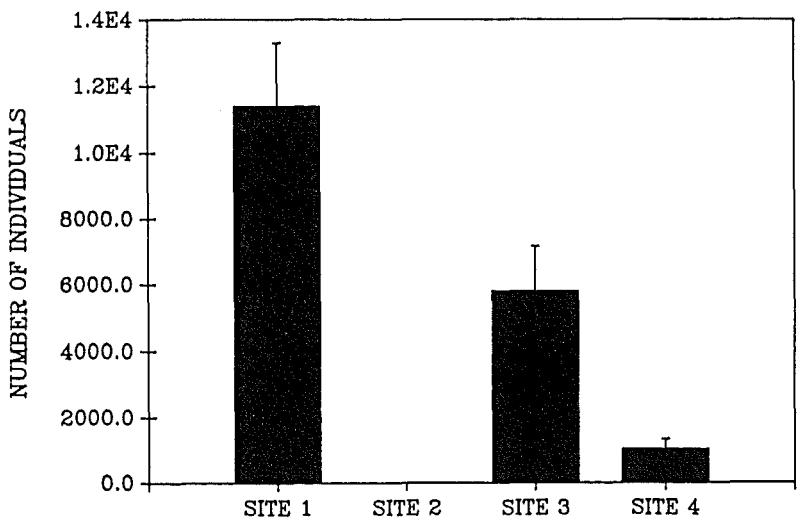
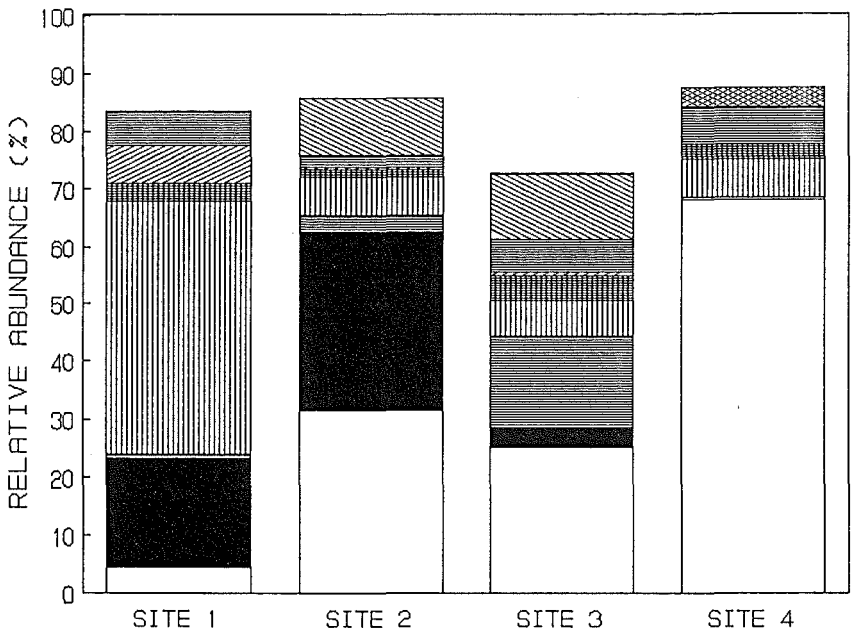


Figure 5. Mean number (± 1 SE) of invertebrates collected from three of the study sites in samples comprising 15 stones taken during the course of the main study (October 1987 - October 1988).



KEY
(□) *Deleatidium* sp. (■) *Potamopyrgus antipodarum* (▤) Simuliidae (▥) *Maoridiamesa harrisi* (▥) ?*Rheocricotopus* sp.
(▤) *Parochlus* sp. (▣) Notoaturinae sp. A (▧) *Pycnocentrodes* sp. (▨) *Aoteapsyche colonica*

Figure 6. Relative abundance of the five most abundant invertebrate species at each of the study sites on 30 May 1987.

whereas site 2, only 100 metres away, was dominated by *Deleatidium* sp., *P. antipodarum* and *Pycnocentrodes* sp. Site 3 was also dominated by *Deleatidium* sp. and *Pycnocentrodes* sp., but *Potamopyrgus* was relatively rare and had been replaced as a dominant by Simuliidae. Site 4 lacked *Potamopyrgus* and *Pycnocentrodes*, and *Deleatidium* sp. was the strongly dominant taxon.

Fig. 7 shows the relative abundance of the top five species in the weed beds.

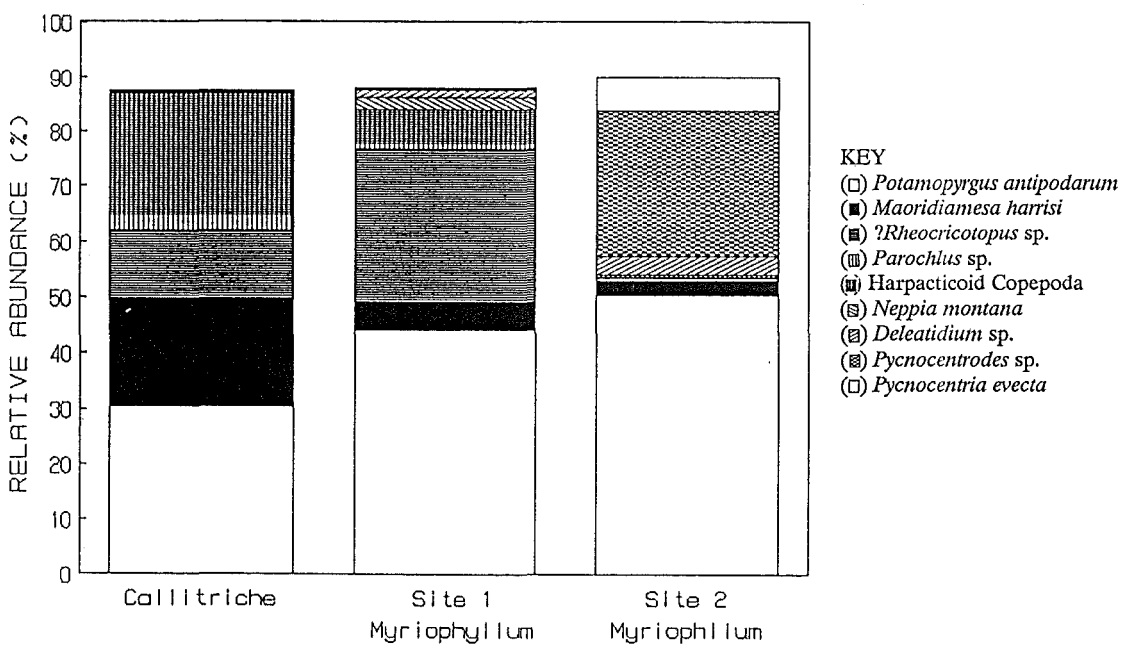


Figure 7. Relative abundance of the five most abundant invertebrate species in 0.02 m^2 samples of *Callitriche stagnalis* and *Myriophyllum* sp. from site 1, and sites 1 and 2, respectively.

These differed on the two species of macrophyte, and interestingly, they also differed between sites on the same species of weed. *Myriophyllum* sp. at site 1 was dominated by *Potamopyrgus antipodarum* and *?Rheocricotopus* sp., whereas at site 2 the dominant invertebrates on *Myriophyllum* sp. were *Potamopyrgus* and *Pycnocentrodes* sp. This was similar to the situation observed in the benthic fauna.

The numbers of taxa and the total numbers of animals collected in samples from site 1 following the removal of the weed by cattle are shown in Figs. 8 and 9.

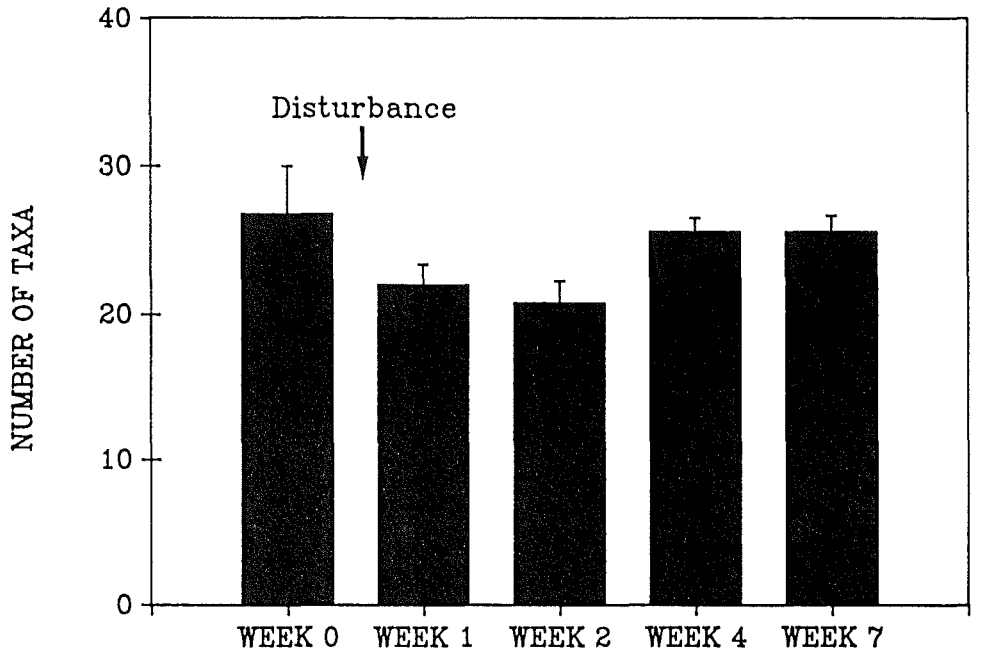


Figure 8. Mean numbers of taxa (± 1 SE) collected in 0.02 m^2 Surber samples before (Week 0) and on four occasions following removal of the macrophyte beds by cattle grazing.

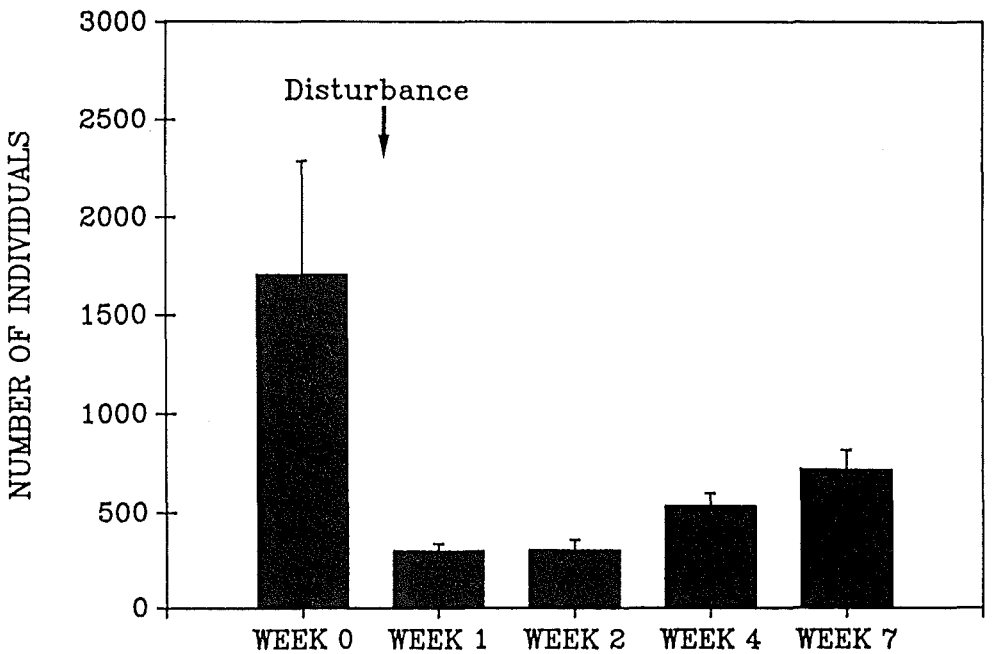
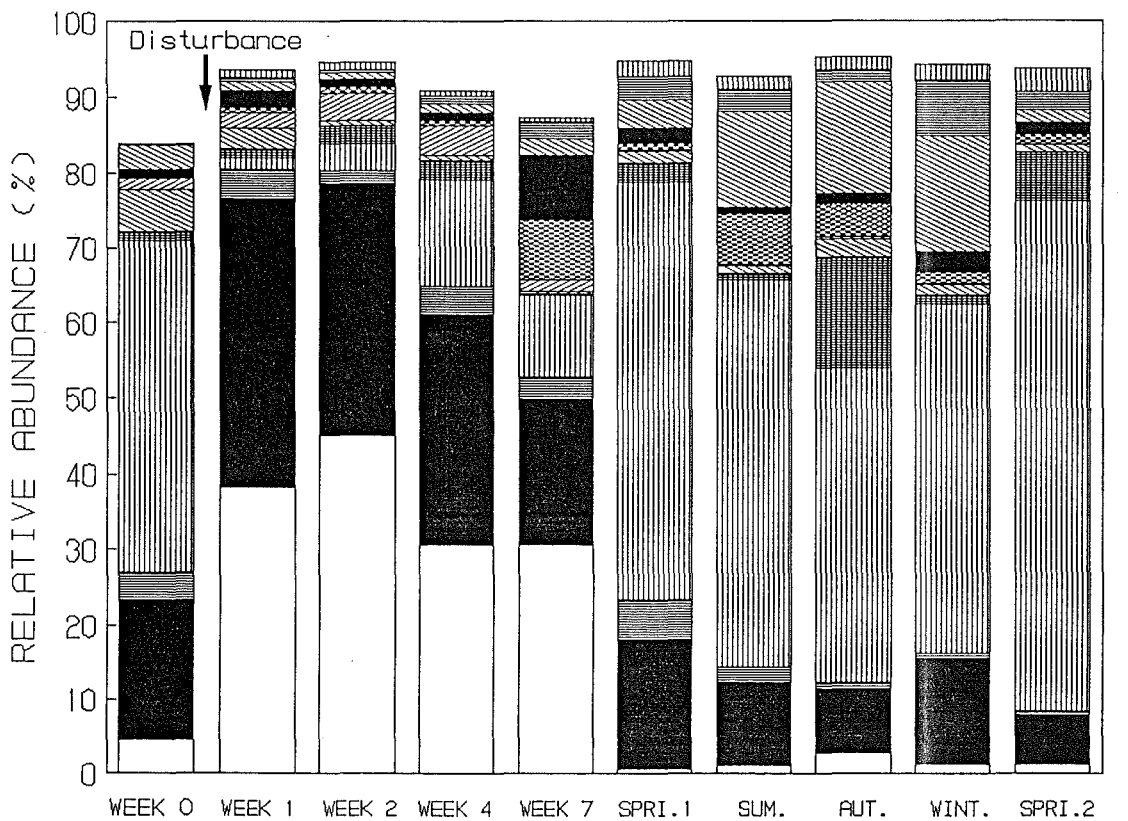


Figure 9. Mean number of invertebrates (± 1 SE) collected in 0.02 m^2 Surber samples before (Week 0) and on four occasions following removal of the macrophyte beds by cattle grazing.

The sample collected from the benthos on 30 May 1987 was used as a measure of predisturbance community structure (i.e., week 0) (although this was a macrophyte community prior to disturbance it was now a strictly benthic community and this seemed a better measure of the community that would develop). The number of taxa present after the disturbance was not significantly different from that present on the stream bed prior to the disturbance (F = 2.06, df = 1,20, P > 0.05). However, the total number of animals taken was significantly lower (F = 9.58, df = 1,20, P < 0.05). Nevertheless, by week 7 total invertebrate density was not significantly different from that observed before the disturbance.

The relative abundances of the five most abundant taxa in the postdisturbance samples are plotted in Fig. 10. Initially, *Deleatidium* sp. and *Potamopyrgus* were dominant but by week 7 their relative abundances were lower and *Maoridiamesa harrisi*, *Slavina* sp. and *Neppia montana* had become more common. The sample taken as part of the main study 20 weeks after the disturbance (although from a



KEY

(□) *Deleatidium* sp.
(▥) *Maoridiamesa harrisi*
(▨) Hydrachenellae sp. C
(▧) *?Rheocricotopus* sp.
(■) *Potamopyrgus antipodarum*
(▩) *Eukiefferiella claripennis*
(▦) *Slavina* sp.
(▤) Hydrachenellae sp. A
(▩) *Paraleptamphopus subterraneus*
(▧) Notoaturinae sp. A
(■) *Neppia montana*
(▦) Harpacticoid Copepoda

Figure 10. Relative abundance of the five most abundant invertebrate species collected in 0.02 m^2 Surber samples following removal of the macrophyte beds by cattle grazing, and in samples comprising 15 stones taken during the course of the main study (October 1987 - October 1988).

site 10 m upstream) indicated communities were returning to their predisturbance composition.

DISCUSSION

Although the conclusions that can be drawn from this study are constrained by the fact that only one sample was collected before two of the sites were severely disturbed, an interesting trend was observed as one moved downstream. Thus, both density and diversity of the invertebrate communities decreased and taxonomic dominance changed. Initially, chironomids and molluscs were dominant, then *Deleatidium* sp., cased caddisflies and simuliids increased in abundance, and finally molluscs and cased caddisflies disappeared and *Deleatidium* sp. became strongly dominant. Similar changes were reflected by the macrophyte fauna as one moved downstream. As hydrological conditions did not appear to be different at the study sites and it is unlikely that water chemistry changed significantly downstream, it seems likely that changes in stability were responsible to a large extent for differences in the communities.

Removal of the weed beds by cattle grazing had the obvious effect of removing the macrophyte fauna, however, the stream bed was rapidly recolonised by benthic invertebrates. Thus, one week after the disturbance the number of taxa recorded was no different from that taken in benthic samples prior to the event, and seven weeks after, total density of invertebrates and relative abundances of invertebrate taxa were beginning to return to predisturbance benthic levels. The weed beds themselves took over a year to return to their original condition.

APPENDIX IV

Fish Gut Analysis

Table 1. Gut analysis of *Anguilla dieffenbachi*.

Taxa	Grasmere Stream								
	A	B	C	D	E	F	G	H	I
Size (mm)	255	252	241	228	210	187	160	137	134
Nematoda	-	2	1	1	1	1	1	1	1
Oligochaeta	5	5	2	-	2	-	-	-	-
Deleatidium sp.	6	4	1	1	8	1	1	4	1
Simuliidae	-	-	1	1	-	2	-	1	-
Maoridiamesa harrisi	-	1	-	-	-	-	-	-	-
Parochlus sp.	-	-	1	-	-	-	-	-	-
Neurochorema sp.	1	-	-	-	-	-	-	1	-
Pycnocentrodes sp.	-	-	-	-	-	-	-	-	1
Terrestrial	-	2	-	-	-	-	-	-	-

Table 2. Gut analysis of *Galaxias brevipinnis*.

Taxa	Kowai River		Porter River	Cora Lynn Stream	Grasmere Stream
	A	B	A	A	A
Size (mm)	61	64	87	73	59
Deleatidium sp.	2	2	5	1	-
Spaniocerca zelandica	-	-	-	1	-
Plecoptera indet.	-	-	-	1	-
Simuliidae	-	-	7	-	-
Maoridiamesa harrisi	1	-	-	-	3
?*Rheocricotopus* sp.	-	-	-	4	-
Eukiefferiella claripennis	1	1	-	-	-
Tanytarsus vespertinus	-	1	-	-	-
Polyplectropus sp.	1	-	-	-	-
Aoteapsyche sp.	-	-	-	-	1
Hydrobiosis sp.	-	2	-	-	-
Costachorema sp.	-	-	1	-	-
Psilochorema sp.	-	1	-	-	-

Table 3. Gut analysis of *Galaxias vulgaris*. + indicates presence of an item not quantified.

Taxa	Kowai River	White Stream			Bruce Stream	Cora Lynn Stream													
	A	A	B	C	A	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Size (mm)	90	81	66	123	91	100	73	86	85	81	74	83	64	70	70	75	73	68	61
Nematoda	-	-	-	5	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Nesameletus sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Deleatidium sp.	1	-	1	5	-	1	2	2	-	1	3	-	1	-	2	2	-	1	-
Adult Ephemeroptera	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zelandobius sp.	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Notonemouridae indet.	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Spanioerca zelandica	-	-	-	-	-	-	-	-	1	-	-	2	-	-	1	1	-	-	-
Elmidae	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scirtidae	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Aphrophila neozelandica	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Tipulidae pupae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Maoridiamesa harrisi	1	-	-	2	-	-	-	-	-	2	-	1	-	-	7	-	-	-	1
?*Rheocricotupus* sp.	-	-	-	-	-	2	12	-	4	14	-	-	-	-	4	-	-	1	2
Eukiefferiella claripennis	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Chironomidae indet.	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	-
Adult Diptera	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aoteapsyche sp.	-	1	1	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hydrobiosella stenocreca	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Hydrobiosis sp.	-	-	-	1	-	-	2	-	1	3	1	-	-	-	1	-	-	-	-
Psilochorema sp.	1	-	-	-	-	-	2	-	1	2	-	-	-	-	-	1	-	-	-
Costachorema sp.	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hydrobiosidae indet.	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Hydrobiosidae pupae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Pycnocentrodes sp.	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxyethira albiceps	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Adult Trichoptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Terrestrial	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-
Wood	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
Beech leaf	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-

Table 4. Gut analysis of *Galaxias paucispondylus*.

Taxa	Bruce Stream						Porter River						
	A	B	C	D	E	F	A	B	C	D	E	F	G
Size (mm)	82	81	64	71	70	69	101	90	86	94	83	83	63
Neppia montana	-	-	-	-	-	-	-	-	-	-	-	-	1
Deleatidium sp.	-	-	2	-	1	1	10	-	3	6	8	4	-
Zelandobius sp	2	-	4	1	1	2	-	-	1	-	1	-	-
Simuliidae	-	-	-	-	-	-	3	-	-	1	3	1	-
Simuliidae pupae	-	-	-	-	-	-	-	-	-	1	-	-	-
Maoridiamesa harrisi	-	-	1	-	-	-	-	-	-	1	-	-	-
?*Rheocricotopus* sp.	-	-	4	-	-	-	-	-	-	-	-	-	1
Chironomidae indet.	-	-	-	1	-	-	-	-	-	-	-	-	-
Neurochorema sp.	-	-	1	-	-	-	-	-	-	-	-	-	-
Costachorema sp.	-	-	-	-	-	-	-	-	-	2	-	-	-
Hydrobiosidae indet.	-	-	1	-	-	1	-	-	-	-	-	-	-

Table 5. Gut analysis of *Gobiomorphus breviceps*. + indicates the presence of an item not quantified.

	Whitewater Stream		Lake Grasmere																
	A	B	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
Size (mm)	6.1	6.7	5.9	5.5					3-4.5										
Physa sp.	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Oligochaeta	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Deleatidium sp.	1	2	-	2	4	6	-	-	1	1	1	-	-	2	-	1	3	-	-
Zelandobius sp.	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	1	-
Limonia nigrescens	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Maoridiamesa harrisi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Eukiefferiella claripennis	1	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	1	-	-
Orthocladiinae sp. B	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-
Adult Diptera	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-	-	-	3	-
Polycentropodidae	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aoteaphsyche sp.	4	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neurochorema sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eggs	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 6. Gut analysis of *Oncorhynchus mykiss*.

	Whitewater Stream		Porter River
	A	B	A
Size (mm)	101	82	89
Deleatidium sp.	28	10	14
Zelandobius sp.	2	1	-
Scirtidae sp.	-	-	1
Blephariceridae	-	1	-
Maoridiamesa harrisi	1	-	1
Limnophora sp.	2	-	-
Aoteapsyche sp.	6	6	-

Table 7. Gut analysis of *Salmo trutta*.

Taxa	Porter River	Slip Spring								Grasmere Stream	Lake Grasmere	
	A	A	B	C	D	E	F	G	H	I	A	A	B
Size (mm)	177	173	155	120	121	102	81	78	70	66	113	36	33
Potamopyrgus antipodarum	-	-	9	-	2	1	-	-	-	-	-	-	-
Oligochaeta	-	-	1	-	1	-	-	-	-	-	1	-	-
Paraletamphopus subterraneus	-	-	1	-	1	-	-	-	-	-	-	-	-
Deleatidium sp.	15	7-	2	-	2	5	2	5	2	6	8	-	3
Zelandobius sp.	-	-	2	1	2	3	1	1	-	-	-	-	-
Adult Plecoptera	-	1	-	-	-	-	-	-	-	-	-	-	-
Archichauliodes diversus	4	-	-	-	-	-	-	-	-	-	-	-	-
Scirtidae sp.	5	1	2	-	-	1	-	3	-	-	-	-	-
Simuliidae	2	-	-	-	-	-	-	-	-	-	-	-	-
Maoridiamesa harrisi	1	-	1	-	3	1	-	-	-	2	-	1	-
?Rheocricotopus sp.	-	-	1	-	-	-	-	-	-	-	-	-	-
Stratiomyidae	-	-	-	-	1	-	-	-	-	-	-	-	-
Limnophora sp.	-	-	-	1	-	-	-	1	-	-	-	-	-
Hydrobiosis parumbripennis	1	1	-	-	-	-	-	-	-	-	-	-	-
Oxyethira albiceps	-	-	-	-	-	-	-	-	-	-	1	-	-
Hudsonema aliena	1	-	-	1	1	1	-	-	-	-	3	-	-
Philorheithrus agilis	-	-	3	1	1	-	-	-	-	-	-	-	-
Beraeoptera roria	-	1	-	-	-	-	-	-	-	-	-	-	-
Olinga feredayi	3	1	-	-	-	-	-	-	-	-	-	-	-
Pycnocentrodes sp.	-	-	-	-	-	-	-	-	-	-	1	-	-
Trichoptera indet.	-	-	-	-	1	-	-	-	-	-	-	-	-
Adult Trichoptera	-	-	-	-	1	-	-	-	-	-	-	-	-
Terrestrial	-	-	2	-	-	-	-	-	-	-	-	-	-
Moss Leaf	-	-	-	-	2	-	-	-	-	-	-	-	-

APPENDIX V

A NEW SPECIES OF *ZELANDOBIUS* (PLECOPTERA: GRIPOPTERYGIDAE: ANTARCTOPERLINAE) FROM NEW ZEALAND

R.G. DEATH

Department of Zoology, University of Canterbury, Christchurch 1, New Zealand.

(Received and accepted 23 May, 1990)

ABSTRACT

Death, R.G. (1990). A new species of *Zealandobius* (Plecoptera: Gripopterygidae: Antarctoperlinae) from New Zealand. *New Zealand Natural Sciences* 17: 23-28.

Zelandobius pilosus n.sp., a hairy species of Gripopterygidae found in the streams of inland Canterbury is described. The adults are easily distinguished from others in the genus by the presence of longitudinal grey markings in the cells of the forewings and by the hairy appearance of the larvae. *Z. pilosus* is particularly unusual in that the adults only appear to emerge in mid-winter.

KEYWORDS: Plecoptera - Gripopterygidae - *Zelandobius pilosus*- new species - New Zealand.

INTRODUCTION

The stonefly genus *Zelandobius* Tillyard is endemic to New Zealand and contains six recognized species (McLellan 1969, 1977). In this paper a distinctive new species is described from material collected from the Porter River and adjacent streams in inland Canterbury. Winterbourn & Gregson (1989) drew attention to the existence of this species whose larvae have a hairy appearance unlike those of any other known species.

DESCRIPTION

ZELANDOBIUS PILOSUS N.SP.

Adult

General colour chestnut brown. Antennae filiform with 31-34 segments clothed in short dark hairs only visible with a light microscope. Length of scape 0.25 mm, pedicel 0.15 mm. Head a uniform chestnut brown with pale ocelli. Segment 5 of maxillary palp twice length of segment 4. Thorax clothed with long hairs predominantly on the pleurites. Pronotum (Fig. 1) rectangular, width:length ratio 1.20-1.55 (mean=1.39), all angles rounded, a paler band at the anterior and posterior ends. The posterior margin of the pronotum is flared upwards giving the appearance of a weakly developed ridge. Metanotum approximately the same width as head (males 1.1-1.4 mm, females 1.2-1.6 mm); mesonotum slightly wider. Legs a lighter brown than thorax, clothed in hairs. Leg measurements as in Table 1. Forewing (Fig. 2) subhyaline with oval, longitudinal grey patches within most cells; maximum width:length ratio 0.24-0.34 (mean=0.28). Number of brown crossveins highly variable (Table 2), even differing between right and left wings of an individual. Hindwing uniformly hyaline. Abdomen chestnut brown with a variable amount of pale patterning in males. Dorsal surface of abdomen in females white and lacking sclerites except on segments 9 and 10 and two small plates on segment 1.

Male Genitalia (Fig. 3-5)

Central sclerite of tergite 10 curved strongly downwards. Posterior sclerite with upturned terminal knob. Epiproct with point varying in shape from a slightly upturned knob to a perpendicular, uniformly tapered point. Paraprocts relatively uniform in width with slight widening at distal end, curved upwards and slightly outwards with a round terminal portion. Sternite 9 with an ovoid sub-genital plate covered in fine transparent hairs. Cerci directed posteriorly and of 9 or 10 segments; basal sclerites directed laterally.

Female Genitalia (Fig. 6, 7)

Sternite 7 sclerotised; sub-genital plate and sternite 9 lacking sclerotisation. Sub-genital plate not extended on to sternite 9; hind margin slightly convex but emarginate medially. Subanal lobes

24 New Zealand Natural Sciences 17 (1990)

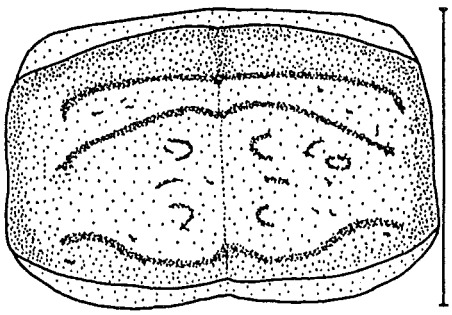


Figure 1. Pronotum. Scale bar = 1 mm.

with weakly pointed apices. Cerci with 7-10 segments.

Larva

General colour sandy brown, becoming progressively darker in later instars. Body and legs covered in long (approx. 0.2 mm) translucent hairs (Fig. 8) that give the animal a shaggy appearance. Most of these hairs are in turn clothed in smaller hairs (Fig. 9), many with only half their circumference covered. The hairs trap detritus and make the larvae difficult to detect in their natural stream environment. Hairiness is greatly reduced in late instars (Fig. 10), which have hairs mainly on wing pads and legs. Head clothed in hairs; epicranium fairly uniformly coloured in earlier instars but with a more mottled appearance in late instars. Antennae filiform, tapering from a wide base to a relatively fine tip; segments becoming progressively elongate towards the distal end. Basal third of flagellum covered in whorls of long hairs similar to those on the body. Labrum without hairs. Ocelli absent or at least not visible with a light or scanning electron microscope. Pronotum rectangular with rounded angles; width:length ratio 1.7-1.9 (mean = 1.8) in middle instars, 1.5-1.8 (mean = 1.7)

Table 1. Mean leg dimensions (mm) (range in parentheses) of male and female *Zelandobius pilosus* (n = 19 specimens).

	MALE			FEMALE		
	Foreleg	Midleg	Hindleg	Foreleg	Midleg	Hindleg
Coxa	0.26 (0.22-0.30)	0.31 (0.25-0.38)	0.36 (0.30-0.38)	0.28 (0.25-0.32)	0.35 (0.28-0.40)	0.42 (0.38-0.48)
Trochanter	0.21 (0.17-0.25)	0.22 (0.17-0.25)	0.23 (0.20-0.25)	0.24 (0.23-0.28)	0.24 (0.22-0.280	0.25 (0.23-0.30)
Femur	1.19 (1.15-1.25)	1.31 (1.25-1.38)	1.93 (1.83-2.10)	1.22 (1.17-1.30)	1.38 (1.25-1.45)	1.96 (1.88-2.00)
Tibia	1.45 (1.38-1.50)	1.59 (1.50-1.83)	2.36 (2.20-2.50)	1.43 (1.25-1.50)	1.64 (1.55-1.75)	2.44 (2.25-2.60)
Tarsus	0.73 (0.68-0.75)	0.76 (0.73-0.82)	0.99 (0.90-1.10)	0.77 (0.70-0.83)	0.80 (0.75-0.90)	1.03 (0.95-1.10)

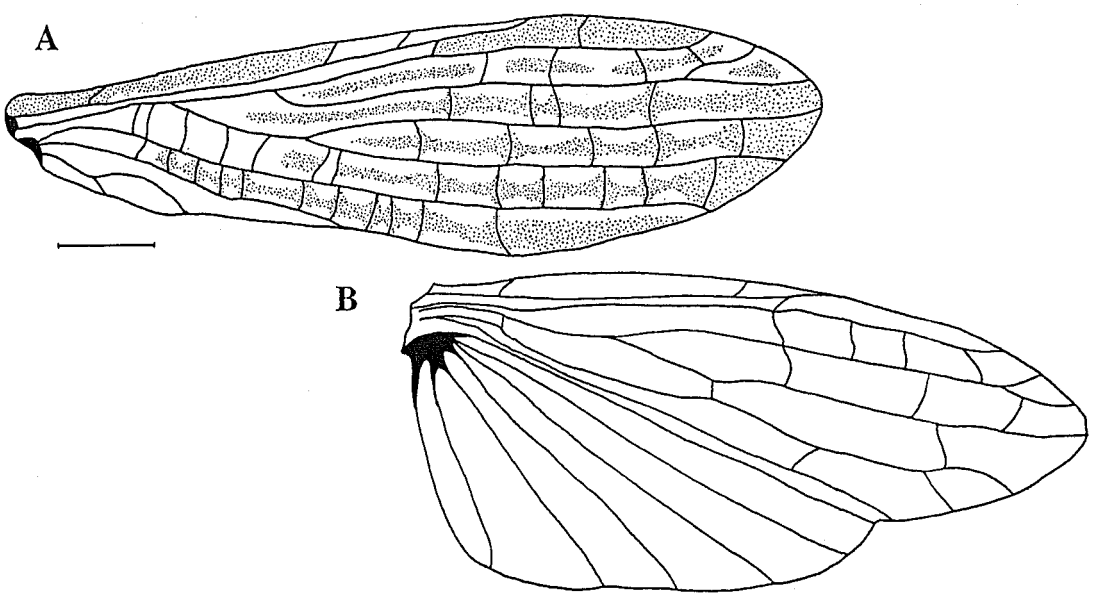


Figure 2. Wings. (A) Forewing. (B) Hindwing. Scale bar = 1 mm.

Table 2. Number of cross veins (mean and range) in the forewings of *Zelandobius pilosus* (n = 25 specimens).

	Mean	Range
Humeral	2.7	1-4
Costal	2.9	1-5
Radial	4.2	3-6
Radio-medial	5.1	3-8
Medial	5.8	4-7
Medio-cubital	10.8	9-13
Intercubital	10.1	8-14

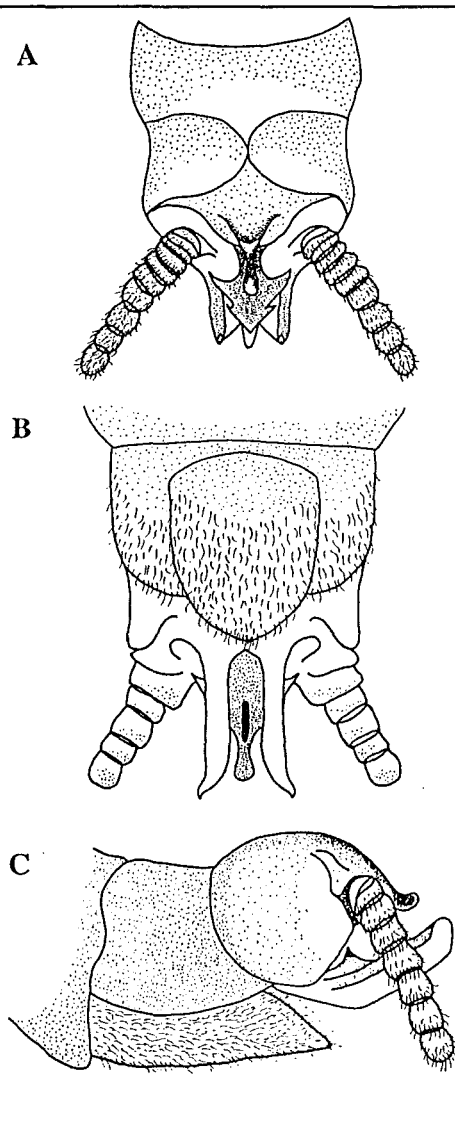


Figure 3. Male genitalia. (A) Dorsal view. (B) Ventral view. (C) Lateral view. Scale bar = 1 mm.

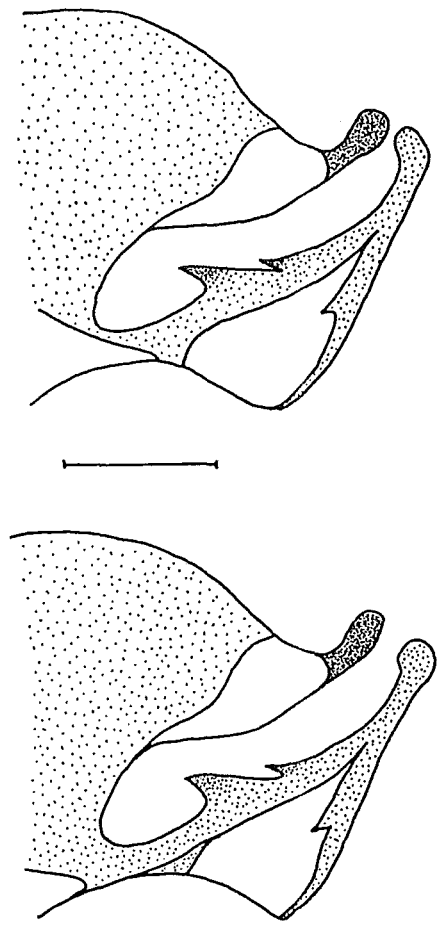


Figure 4. Lateral views of male tergite 10 and epiproct to show variability in shape of terminal point. Scale bar = 0.1 mm.

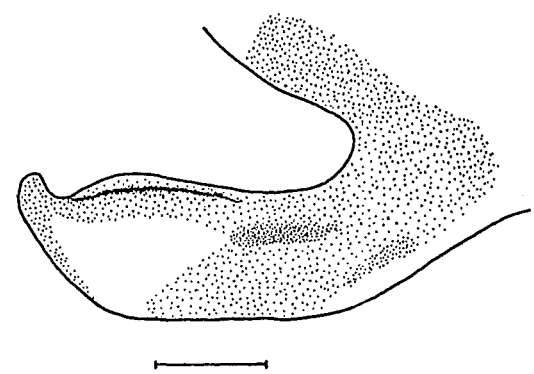


Figure 5. Lateral view of paraproct. Scale bar = 0.1mm.

26 New Zealand Natural Sciences 17 (1990)

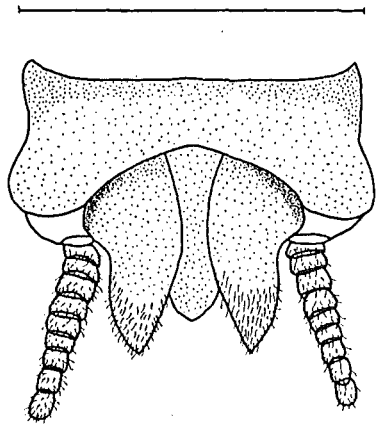


Figure 6. Female genitalia, ventral view. Scale bar = 1 mm.

in late instars. Pronotal hairs best developed around the periphery. Anterior and particularly posterior margins of pronotum slightly curved up so as to give the impression of a weakly developed ridge. Meso- and metanota thickly covered in hairs; hind margins of both plates straight. Legs clothed in hairs; tarsal claws long. Tibiae slightly longer than femora. Abdomen without a dorsal longitudinal ridge. A pale rectangular patch on abdominal tergites 5-9 is distinct in late instar larvae but less so in earlier instars. Tergite 10 weakly pointed and darker along its posterior edge. Cerci thread like, about half length of abdomen. Anal gill rosette well developed. Subanal lobes tongue shaped.

First instar larva

Body length 0.60-0.65 mm. Head width 0.21 mm. Eyes not visible. Antennae with 7-8 segments. A few long hairs present on body. Abdomen covered in short spines about 7 μm long. Cerci 4-segmented.

Egg

Eggs are roughly spherical (Fig. 11), 0.3 mm diameter, with tuberculate sculpturing (Fig. 12).

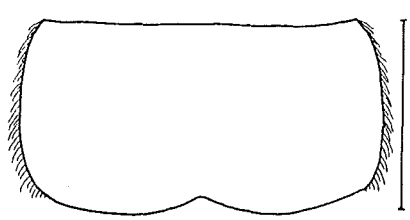


Figure 7. Female sub-genital plate. Scale bar = 0.5 mm.

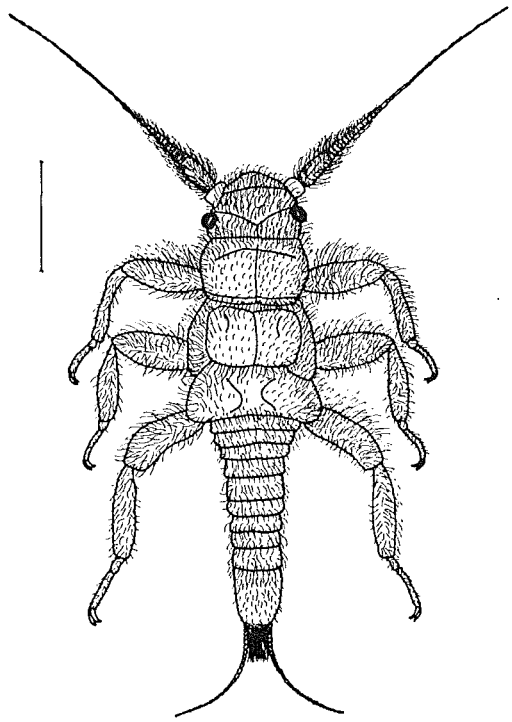


Figure 8. Middle instar larva. Scale bar = 1 mm.

Field collected adults laid the eggs in batches of 45-156, in petri dishes of water in the laboratory. Sometimes batches of eggs formed a coherent mass, 1 layer of eggs deep, which was stuck to the bottom of the petri dish with a jelly-like substance; other eggs were laid singly. Hatching of eggs occurred synchronously after 6 weeks at 5°C.

DIFFERENTIAL DIAGNOSIS

Adults clearly distinguished from others of the genus by the presence of longitudinal grey markings in cells of the forewings. Pronotum most similar to *Z. illiesi* with width:length ratio of 1.2-1.55, but lacking any spines or acute angles. Epiproct of male with a pair of teeth on each outer margin as in type species (*Z. confusus* (Hare)). Paraprocts with a blunt terminal tip unlike those of *Z. confusus* which terminate in a dorsally directed tooth. Cerci directed posteriorly with laterally directed basal sclerite similar to *Z. furcillatus* and *Z. unicolor*. Cerci shorter than in type species but similar to all others in the genus with 9-10 segments. Female sub-genital plate most similar to type species. Female cerci similar in length to oth-

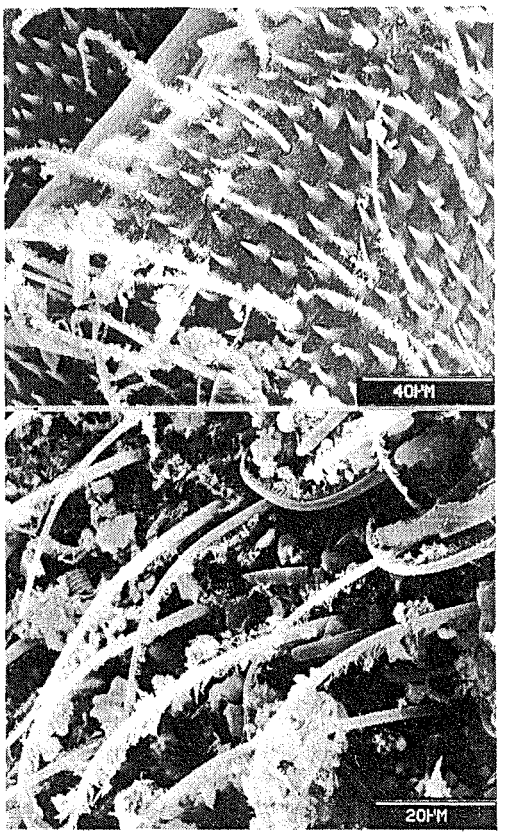


Figure 9. Scanning electron micrographs of hairs on pleurite of abdominal segment 5 of middle instar larva. (Note. The larva was placed in an ultrasonic cleaner for 10 s to remove some of the detritus and make viewing easier).

ers in genus except type species, with 7-10 segments.

Larvae are clearly distinguished from others in the genus by their very hairy appearance. Pronotum rectangular (width:length ratio 1.7-1.9) and most like that of *Z. furcillatus*. Antennae resembling those of *Z. illiesi* with basal portion covered in whorls of hairs. Hind margins of meso- and metanota straight unlike others in the genus. Abdomen lacking dorsal ridge found in *Z. furcillatus* and *Z. unicolor*. Tergite 10 longer and more pointed than in type species, but similar to others in the genus. Cerci short and thread-like, most similar in length to *Z. unicolor*.

ETYMOLOGY

The specific name *pilosus,* (Latin for 'hairy') refers to the very hairy appearance of the larvae.

MATERIAL EXAMINED

Type material: Holotype♂ : New Zealand, MC, Porter River, 732 m a.s.l., 27 Jun 1987, R.G. Death, NZAC. Paratypes: 1♂, 2♀♀, MC, Dry Stream, 16 Jun 1987; 6♂♂3♀♀, MC, Porter River, 27 Jun 1987, 4 Aug 1987 and 5 Jun 1988, R.G. Death; 8 mid instar larvae, MC, Porter River, 7 Mar 1990, R.G. Death, NZAC, AMNZ, NMNZ CMNZ. Other material examined 28♂♂19♀♀MC, Porter River, 19 Jun 1987, 27 Jun 1987 and 4 Aug 1987, R.G. Death; 7 late instar larvae, MC, Porter River, 16 Jun 1987, R.G. Death; 2 mid instar larvae, MC, Porter River, 7 Mar 1990, R.G. Death.

NOTES ON BIOLOGY

All larvae were collected from small to medium sized streams in the Cass-Porter Heights region of inland Canterbury where they can occur in quite high densities. Although observations were made throughout the year, adults were only found during winter (June-August) when snow can lie on the ground for short periods, and air temperatures regularly fall below zero. Adults collected from the wild had no particulate materials in their guts but fed readily on sugar solution in the laboratory. Larvae appear to feed predominantly on detritus and periphytic algae although animal remains were found in guts of some late instar larvae.

DIMENSIONS OF ADULTS AND LARVAE (mm)

	Male	Female	Late instar larvae	Mid instar larvae
	(n=36)	(n=24)	(n=7)	(n=10)
Body length	7.0-8.8 ($\bar{x}$=7.9)	9.3-10.6 ($\bar{x}$=9.8)	6.9-9.3 ($\bar{x}$=8.2)	3.7-4.3 ($\bar{x}$=4.2)
Head width			1.12-1.43 ($\bar{x}$=1.31)	0.92-0.97 ($\bar{x}$=0.94)
Forewing	8.0-9.0 ($\bar{x}$=8.4)	9.4-10.4 ($\bar{x}$=9.8)		
Antenna	5.8-7.2 ($\bar{x}$=6.4)	6.0- 7.9 ($\bar{x}$=6.9)	2.9-4.2 ($\bar{x}$=3.7)	2.0-2.8 ($\bar{x}$=2.5)
Cercus	0.43-0.58 ($\bar{x}$=0.50)	0.5-0.65 ($\bar{x}$=0.58)	0.8-1.1 ($\bar{x}$=0.9)	1.0-1.3 ($\bar{x}$=1.3)

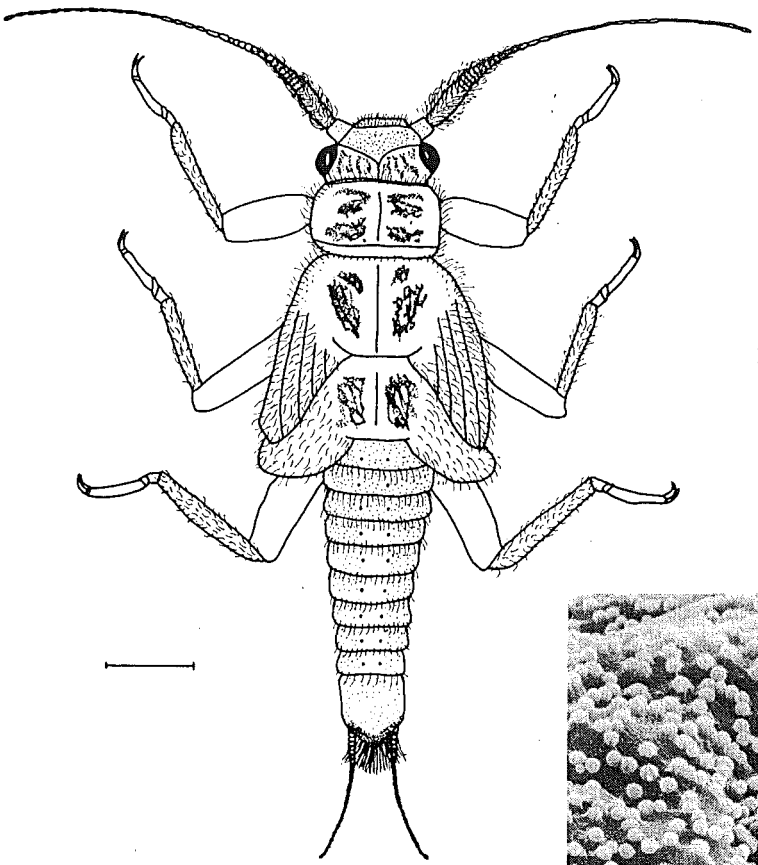


Figure 10. Late instar larva. Scale bar = 1 mm.

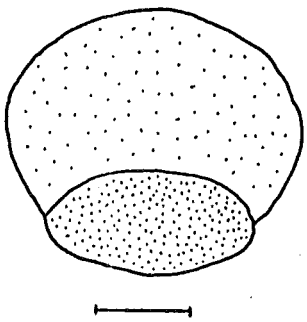


Figure 11. Egg. Scale bar = 0.1 mm.

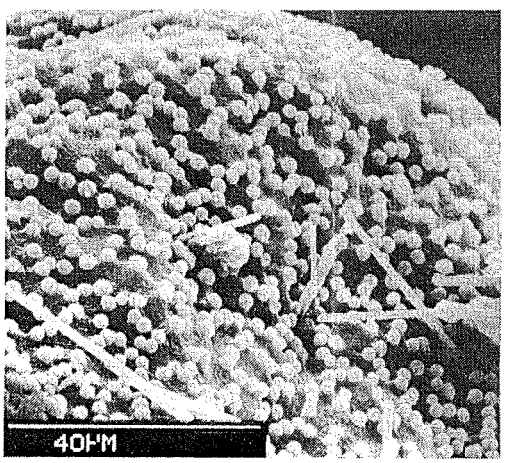


Figure 12. Scanning electron micrograph of egg showing surface sculpturing.

ACKNOWLEDGEMENTS

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REFERENCES

McLellan, I.D. (1969). A revision of the genus *Zelandobius* (Plecoptera: Antarctoperlinae). *Transactions of the Royal Society of New Zealand, Biological Sciences* 11(3): 25-41.

McLellan, I.D. (1977). New alpine and southern Plecoptera from New Zealand, and a new classification of the Gripopterygidae. *New Zealand Journal of Zoology* 4: 119-147.

Winterbourn, M.J. & Gregson, K.L.D. (1989). Guide to the Aquatic Insects of New Zealand. *Bulletin of the Entomological Society of New Zealand* 9.